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COVER: White-throated Hawks (*Buteo albogularis*). Painting by Carlos Kovacs.

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BREEDING BIOLOGY AND NEST CHARACTERISTICS OF THE WHITE-THROATED HAWK (*BUTEO ALBICULA*) IN NORTHWESTERN ARGENTINE PATAGONIA

ANA TREJO¹

Centro Regional Bariloche, Universidad Nacional del Comahue, 8400 Bariloche, Río Negro, Argentina

VALERIA OJEDA

Centro Regional Bariloche, Universidad Nacional del Comahue, 8400 Bariloche, Río Negro, Argentina

Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina

LORENZO SYMPSON

Sociedad Naturalista Andino Patagónica, Pasaje Juramento 190 3°1, 8400 Bariloche, Río Negro, Argentina

MARIANO GELAIN

Lanín 3541, Barrio Melipal, 8400 Bariloche, Río Negro, Argentina

ABSTRACT.—We studied the breeding biology of the White-throated Hawk (*Buteo albicula*) in *Nothofagus* forests of northwestern Argentine Patagonia. We documented 11 nesting attempts from September to April 1998–2002, and recorded behavioral observations at two nests during the 2001–02 breeding season. After the hawks' arrival in the area in mid-September, the pre-laying period extended approximately until early November (ca. 1.5 mo). Laying at two nests occurred between 10 and 15 November. Incubation lasted until 15–17 December (ca. 1 mo). The brood rearing period (ca. 40 d) extended until late January, when fledging was observed. However, in one nest in the 2000–01 season, we found a small chick on 13 January that fledged about 20 February, which suggests that some late breeding attempts can be successful. Females performed most of the incubation. Pairs produced only one fledgling per successful nest, but we observed two nestlings during the early brood-rearing stage at one nest. Both sexes defended nests against intruders. Males delivered all of prey brought to the nests during incubation, and 80% of food delivered during the nestling period. Birds, rodents, and lizards were the most numerous prey brought to nests. White-throated Hawk nests were platforms made of dry and green sticks located at a mean height of 16 m above the ground in *Nothofagus* trees that averaged 0.8 m in diameter at breast height.

KEY WORDS: *White-throated Hawk; Buteo albicula; breeding biology; nests; northwestern Patagonia; Argentina.*

BIOLOGÍA REPRODUCTIVA Y CARACTERÍSTICAS DE LOS SITIOS DE NIDIFICACIÓN DEL AGUILUCHO ANDINO (*BUTEO ALBICULA*) EN EL NOROESTE DE LA PATAGONIA ARGENTINA

RESUMEN.—Estudiamos la biología reproductiva del aguilucho andino (*Buteo albicula*) en bosques de *Nothofagus* del noroeste de la Patagonia argentina. Documentamos 11 intentos de nidificación desde septiembre a abril de 1998–2002, y registramos observaciones de comportamiento en dos nidos durante la estación de cría 2001–02. Luego de la llegada de los aguiluchos al área a mediados de septiembre, el período previo a la postura se extendió hasta principios de noviembre (aproximadamente un mes y

¹ E-mail address: strix@bariloche.com.ar

medio). La postura en 2 nidos tuvo lugar entre el 10 y el 15 de noviembre. La incubación se prolongó hasta el 15–17 de diciembre (alrededor de un mes). El período de crianza en el nido se extendió hasta fines de enero, cuando los volantones abandonaron el nido (aproximadamente a los 40 días de edad). Sin embargo, en uno de los nidos durante la temporada reproductiva 2000–01, encontramos un pichón el 13 de enero que voló aproximadamente el 20 de febrero, lo que sugiere que la reproducción puede retrasarse ocasionalmente con éxito. Las hembras llevaron a cabo la mayor parte de la incubación. Las parejas produjeron sólo un volantón por nido exitoso, aunque en uno de los nidos observamos dos pichones al comienzo del período de crianza. Ambos sexos defendieron los nidos contra los intrusos. Los machos aportaron el 100% de las presas durante la incubación, y el 80% durante el período de crianza en el nido. Las presas llevadas a los nidos fueron principalmente aves, roedores y lagartijas. Los nidos del aguilucho andino se encontraban en promedio a 16 m sobre el terreno en árboles de *Nothofagus* de 0.8 m de diámetro a la altura del pecho. Todos los nidos eran plataformas construidas con ramas secas y verdes.

[Traducción de los autores]

Among Neotropical birds, raptors are one of the least studied groups and relatively little is known about their breeding biology (Bierregaard 1998). The White-throated Hawk (*Buteo albogularis*) is distributed along the Andes, ranging from southern Argentina and Chile to Bolivia, Peru, Ecuador, Venezuela, and Colombia (del Hoyo et al. 1994). In Argentina, this hawk inhabits the southern beech (*Nothofagus* spp.) forests of western Patagonia (40°02'S–42°51'S; Gelain et al. 2001), and the northwestern part of the country (Olrog 1979, Caneveri et al. 1991). Little is known about the biology of the White-throated Hawk. Pavez (2000) recorded migratory movements of White-throated Hawk flocks from south to north in autumn (March–May) and from north to south in the spring (September–October) in central Chile. Recently, breeding pairs were located in northwestern Patagonia, from early September through early April (Gelain et al. 2001), and first description of nests were published (Trejo et al. 2001). Also Figueroa et al. (2001) described movements and hunting strategies of hawks in southern Chile. Our study summarizes information on breeding biology, behavior, and nests of this forest raptor collected during 4 yr in northwestern Argentine Patagonia.

METHODS

We studied White-throated Hawks in the vicinity of Bariloche city (41°08'S, 71°12'W), northwestern Argentine Patagonia. Physiographically, the area consists of lakes, glacial valleys, and mountain slopes covered by forests dominated by southern beech. Elevation ranges from 400–3480 m. Mean annual temperature is 8°C and total annual rainfall ranges from 500–2000 mm, mainly concentrated in winter (Paruelo et al. 1998). Predominant winds come from the west.

We conducted fieldwork during four breeding seasons (September–April 1998–2001) in four nesting territories

used by breeding pairs in consecutive years. For a general description of these sites, see Gelain et al. (2001). Throughout breeding season, we (at least once a week) made periodic visits and recorded the activities of territorial pairs. Early-season observations were made from vantage points to determine the probable locations of nests. We located occupied nests by following adults carrying nest material or food, and by noting the aggressive diving behavior of one or both members of the pair when we approached the nest site. Thereafter, we visited the nests every 1–2 wk (sometimes more often), and recorded activities and behavior observed. Binoculars and a 20–60× spotting scope were used throughout the study.

We defined a nest as occupied when it contained young or when an adult was seen in the nest incubating. We classified a nest as successful if at least one young was fledged.

We observed the hawks' daily routine in two nests (N1 and N2) throughout the 2001–02 breeding season (15 November 2001–24 January 2002). These two nests were located in the Challhuaco River Valley, 15 km southeast of Bariloche. This is a rugged area covered by 1900 ha of pure old-growth deciduous lenga (*Nothofagus pumilio*) forest averaging 15 m tall, located at 900–1650 m above sea level. The understory is open, dominated by small bushes (primarily *Ribes magellanicum*, *Berberis serratodentata*, *Schinus patagonicus*), and annual herbs (*Alstroemeria aurea* was most common). Observations at these two nests were carried out once a week, and were made from dawn to dusk (0600–2100 H). We monitored the nests from 29 November–27 January (2 wk during incubation and 5 wk during the brood-rearing period) for a total of 210 hr. Observations were made from ground blinds at distances of 20–25 m from the nest tree.

For both adults at each nest we recorded the birds' activity, time and duration of the activity, and a description of any associated behavior. We classified behaviors into the following categories: incubating, attending nest, feeding young, in vicinity, and absent. The "attending nest" category included the perching, preening, stretching, resting, feeding, adding nest material, or anything else, but not incubating or feeding nestlings. "In vicinity" refers to the amount of time an adult was perching in the nesting territory, or flying from perch to perch, or was present in the nest neighborhood (included visual and vocal detections). Activities 20–30 m away from the

nest could not always be seen clearly due to the presence of a dense canopy. All prey items delivered to the nest were identified to Class or Order whenever possible. Daily feeding rates were calculated excluding days when no feeding events were observed. Twigs carried to the nest were classified as green or dry, based on the presence/absence of leaves.

We marked one adult of each pair monitored during 2001–2002 breeding season. Shortly after nests were located, we trapped one male with the aid of a bal-chatri trap baited with a hamster, and one female with a dhogaza net and a stuffed Magellan Horned Owl (*Bubo magellanicus*) (Bloom 1987). Birds were ringed with uniquely-numbered aluminum bands. Gender of captured hawks was determined by size comparison and behavior (e.g., incubation).

After young fledged or the nest failed, we climbed to the nest trees to describe and measure the platforms. We recorded the following microhabitat variables: nest-tree species, nest-tree height (with an optical range finder), nest-tree diameter at breast height (DBH, with diameter tape), nest tree condition (live, partly dead, or dead), nest height (measured in plumb-line distance from the nest to ground level using a measuring tape), distance from the inner edge of the nest to the main axis of the nest tree, and nest compass orientation relative to that tree axis (deviation from magnetic north grouped in 45° octants). We also measured elevation with an altimeter, slope (%) with a clinometer, and compass aspect of the nest sites. Distance between occupied nests was only estimated (using Global Positioning System, [GPS] coordinates and receiver) for N1 and N2, the only breeding territories that were likely adjacent.

RESULTS

We located one occupied nest in 1998, one in 1999, four in 2000, and five in 2001 (including one renesting attempt) in the four nesting territories. Eight of the 11 occupied nests (72%) were successful and all fledged one young.

Two nests were located at the pre-laying stage, six at the incubation stage, and three during the brood-rearing period.

Pre-laying Period. The pre-laying period extended approximately from mid-September until early November (ca. 1.5 mo). The pairs were observed around their nesting territories in early October, when one or both adults flew by us in a non-aggressive manner, generally responding to play-back calls and then flying off. Closer to laying date, birds usually became very attached to the nest site, but still showed no aggressiveness. Behaviors observed in this period were undulating-flight displays, copulations, and nest-building activities. Six undulating displays were observed (12 October–29 November) during the pre-laying period and early incubation, in different pairs/seasons, all performed by the male in the presence of the female

(except one). Nest-building activities, which were recorded only twice during this period, continued throughout the incubation and brood-rearing stages, when they increased noticeably.

We witnessed eight copulations of five different pairs/seasons, between 17 October and 17 November. These always took place on dead trees or dead branches adjacent to nest trees. Copulations were not preceded by any discernible courtship behavior except vocalizations from both members of the pair. Once, copulation followed a territorial defense by the pair against a Red-backed Hawk (*Buteo polyosoma*).

Incubation Period. We observed incubation activities at six nests. One of these nests failed, leaving an egg which measured 50.23 × 39.98 mm, was white, without gloss or spots, only showing some brownish stains (Fig. 1). Egg fragments found at another nest were also totally white and without gloss on the outer side, and bluish inside.

At N1 and N2, laying was initiated about 10–15 November, and incubation continued until 15–17 December (ca. 1 mo). During our daily observations at N1 and N2 during 2 wk, most of daytime incubation was done by the female, but we recorded some incubation by the male (Table 1). During daytime both members of the pair took turns at incubating. The male's shifts varied from 13 min–2 hr 30 min, and averaged 57 min ($N = 7$ shifts). When incubating, the adult frequently turned the eggs. Close to the hatching day, females increased their incubation time to 100%. Females were always seen on the eggs at dusk and at dawn, and presumably incubated at night. Males were not usually seen near the nest while females incubated, but they would come quickly when females called.

Of the observed prey delivered to N1 and N2 during incubation ($N = 8$), 37.5% were rodents, 25% lizards, and 37.5% unidentified. All of the prey delivered to the nest or perches nearby during incubation was brought by the males. Females generally (87.5%, $N = 8$) ate the prey at the nest (where males had left the prey after flying directly onto the platform), less frequently she ate the prey at an exchange perch nearby (usually, a large horizontal branch), while the male replaced her at the nest. Feeding rate during incubation averaged 2 times/day ($SD = 1.4$, range = 1–4, $N = 4$ d). During incubation, nest material was mostly added by the female (Table 2).

Brood-rearing Period. The brood-rearing period was monitored at the eight nests where nestlings



Figure 1. White-throated Hawk egg found in one nest in Challhuaco River Valley, Bariloche, northwestern Argentine Patagonia.

Table 1. Percentage of total daylight time spent by each gender exhibiting various behavior activities through the 2001–02 breeding season at two nests (N1 and N2) of the White-throated Hawk in the Challhuaco River Valley, northwestern Argentine Patagonia. I to VII correspond to observation weeks after hatching. F = females and M = males.

ACTIVITY	INCUBATION								NESTLING PERIOD							
	I		II		III		IV		V		VI		VII			
	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Nest N1																
Incubating	86.8	31.3	93.2	0	0	0	0	0	0	0	0	0	0	0	0	0
Attending nest	3.2	0	4.7	0.9	79.0	0	24.6	0	16.3	0	4.2	0	0.63	0		
Feeding young	0	0	0	0	2.7	0	1.2	0	0.7	0	1.3	0	0	0		
In vicinity	0	4.2	2.1	17.6	6.7	13.0	70.0	10.0	69.0	19.3	62.3	10.9	88.5	3.1		
Absent	10.0	64.5	0	81.6	11.8	87.0	4.3	90.1	14.0	80.7	32.2	89.1	10.9	96.9		
Nest N2																
Incubating	84.7	9.3	92.2	—	—	—	—	—	—	—	—	—	0	0		
Attending nest	1.5	1.4	7.3	0.3	84.9	—	42.4	12.8	19.9	—	3.2	—	0.6	—		
Feeding young	—	—	—	—	9.9	—	3.6	—	6.4	—	—	—	—	—		
In vicinity	0.9	—	0.4	3.9	1.4	2.7	22.6	7.8	56.6	8.3	77.6	8.7	56.2	8.0		
Absent	12.9	89.3	—	95.8	3.8	97.3	31.4	79.4	17.1	91.7	19.2	91.7	43.3	92.1		

Table 2. Twig deliveries by White-throated Hawks to nests N1 and N2 during the 2001–02 breeding season in the Challhuaco River Valley, northwestern Argentine Patagonia.

	INCUBATION				NESTLING PERIOD			
			UNIDEN-	TOTAL			UNIDEN-	TOTAL
	GREEN	DRY	TIFIED		GREEN	DRY	TIFIED	
Males	1	0	0	1	0	3	0	3
Females	2	0	0	2	18	11	2	31
Unidentified	0	0	1	1	2	1	0	3
Total	3	0	1	4	20	15	2	37

were observed. At nests N1 and N2, this period began on 15–17 December, and extended approximately for 5–6 wk, dates that were comparable to those observed (or inferred) for the other nests. Brood size was one, except for one nest where two chicks were seen during the first week after hatching, but only one was seen thereafter.

At N1 and N2, nestlings were normally brooded by females during the early and late hours of the day (and presumably overnight) until week 4, after which the females probably roosted nearby. Because of the extreme range in daily temperature (5–30°C) during the breeding season in northern Patagonia, the adults (usually the female) varied their postures from sitting tightly and covering the nestling completely to standing over and shading the chick from the sun.

Male visits to the nest were nearly always limited to food deliveries, and his attendance declined during the brood-rearing period (Table 1). Female attendance also diminished through the nestling period, but not as markedly, and she mostly remained in the vicinity of the nest until the juvenile fledged (Table 1). During the last 2 wk of the brood-rearing period, the female visited the nest exclusively to feed the nestling or to deliver prey, and to add and arrange nest material.

Of prey brought to nests N1 and N2 or to the vicinity ($N = 31$), 26% were birds, 16% rodents, 13% lizards, and 45% unidentified. Eighty percent of total prey were brought to nesting areas by the male, 10% by the female, and 10% by an unidentified adult. For 69% of the food deliveries the adult flew directly to the nest with prey, and in 31%, the male flew into the nest vicinity and the female flew to meet him on a perch.

We observed 25 prey deliveries to the nestlings. Chicks were fed by females (84%), males (4%), or consumed the prey by themselves (12%). The

mean feeding frequency was 3.22 prey deliveries/day ($SD = 1.9$, range = 1–6, $N = 10$ d). Food was provided at a mean interval of 4 hr 39 min ($SD = 2$ hr 4 min, range = 10 min–12 hr 50 min, $N = 11$) and the feeding sessions lasted 10 min ($SD = 6.7$, $N = 17$), on average. Soon after hatching, chicks could consume morsels, being frequently assisted by the adults (usually the female), who gave them small pieces of meat without skin, feathers or hard body parts. At the age of 4 wk, the chicks attempted to dismember prey by themselves.

No feeding was observed during the week before fledging. Two prey brought by the male at N1 were consumed by the female without sharing them with the nestling. In one of these cases, the prey was carried to the nest, where the nestling tried unsuccessfully to take a piece.

Compared with the incubation period, females at N1 and N2 abruptly increased their nest building activities during the brood-rearing period (Table 2).

At the age of ca. 35 d (ca. 1 wk prior to fledging), when adults were rarely present, the chick moved around the nest and onto nearby limbs to seek shade during hot hours or to bask in the sun during cold hours. Sometimes nestlings moved 3–4 m above and beyond the nest in branches, occasionally hopping and fluttering back to the nest. Also, we heard young calling commonly with subtle chirps, which only sometimes resulted in a response from adults.

Post-fledgling Period. Post-fledgling behavior was described exclusively on incidental observations. Juveniles were always seen with one or two adults (presumably, its parents) flying above the canopy near their nesting territory, or high above adjacent open land. Feeding by juveniles was observed five times in the post-fledgling period. Three times we recorded an adult delivering ro-

Table 3. Characteristics of White-throated Hawk nests and nest trees in northwestern Argentine Patagonia.

	MEAN \pm SD (N)	RANGE
Height of nest above ground (m)	16.2 \pm 3.3 (7)	13.0–22.0
Distance of nest to main tree bole (cm)	0.5 \pm 0.9 (7)	0–2.4
Tree height (m)	20.6 \pm 3.3 (7)	16.5–25.0
Tree DBH (m)	0.8 \pm 0.2 (6)	0.5–1.1
Nest position relative to tree height (%)	78.1 \pm 9.7 (7)	95–91

dent prey to a tree perch, then flying off immediately before the juvenile went to the perch to eat. On one occasion we observed an adult passing prey to a juvenile directly in the air. Another time we saw a juvenile eating a rodent (head first) it held in its claws on a perch.

Nests. Three of the 11 occupied (27%) nests were reused in successive breeding seasons. Besides, we found an abandoned and seemingly very old, bulky nest in 2000 that was attributed to White-throated Hawks because of its similarity in appearance and it was located near two confirmed nests (65 and 9 m, respectively). All nests were placed on *Nothofagus* trees, nine in lenga and one in a coihue (*N. dombeyi*). All nests were built in live trees, except one in a mostly dead tree with some few small living branches. The elevation of the nest tree sites averaged 1139 m (SD = 159, range = 924–1350 m, N = 6), and slope averaged 21% (SD = 14, range = 4–44, N = 6). Nest-tree sites did not show a definite slope orientation, three were facing west, two north, and one south. The number of alternate nests within breeding territories ranged from 1–3, averaging 2 (SD = 0.8, N = 4). Mean distance between alternate nests within a territory was 178 m (SD = 118 m, range = 60–310 m, N = 5). Distance between occupied nests N1 and N2 was 2 km.

Nests were platforms placed on forked branches in the mid-upper part of, generally, large trees (Table 3). They were firmly secured to the branches, and were almost always hidden from the ground. Materials used for nest building consisted exclusively of twigs and sticks belonging to the species of *Nothofagus* dominant at the site. Dry sticks formed the perimeter of the nests, and green ones lined the inner cup (Fig. 1). Sticks were 0.6–1.4 cm

Table 4. Morphometrics of White-throated Hawk nests in northwestern Argentine Patagonia. Repeated numbers indicate a nest that was reused during the study period.

NEST	NEST DIAMETER (cm)	CUP DIAMETER (cm)	DEPTH OF NEST	
			CUP (cm)	NEST (cm)
1	72 \times 68	25 \times 24	7	26
1	77 \times 63	21 \times 16	3	37
2	80 \times 76	36 \times 30	8	22
3	66 \times 65	19 \times 17	5	45
4	77 \times 38	30 \times 31	2	22
5	67 \times 62	23 \times 20	6	37
6	78 \times 70	25 \times 23	5	30
6	81 \times 67	22 \times 21	7	40
7	67 \times 57	22 \times 20	3	24
7	61 \times 55	20 \times 18	8	32
Means ¹	72.43 \times 62.28	25.71 \times 23.57	5.14	29.43

¹ Nests reused were included only once; the first measurements were used to calculate means.

diameter, and 50–70 cm length. Both kinds of twigs (green and dry) were covered by lichen and moss.

Nest platforms were fairly variable in shape, size, height, and orientation with respect to the axis of the nest tree, but most of their remaining features (as architecture) were more or less homogeneous (Table 4). Differences in size, mainly thickness, seem to be mostly related to the age of the nests and number of times they were used. As we believe that the dimensions of preexisting nests impose a constraint on the size of reused nests, we present data on nests separately and did not average dimensions for nests used more than once (Table 4). A nest found under construction in 2001 (not included in Table 4) was noticeably smaller than the average occupied nest, with maximum dimensions 54 \times 50 cm. Three nests faced north, two faced southeast and the remaining nests faced east, west, southeast, and northwest. This orientation was not skewed, but our data is insufficient to test for distribution patterns.

DISCUSSION

There is no previous information on the breeding period of the White-throated Hawk, but our data for this species are consistent with the general patterns reported in the literature for other *Buteo* hawks of similar size.

We could not confirm clutch size at the occupied

nests. Regardless of clutch size, overall breeding success, measured in the number of nestlings raised to fledging per successful nest was one, which seems to be relatively low for a *Buteo* in temperate zones (del Hoyo et al. 1994). We elected not to climb nest trees during incubation to avoid disturbing the hawks. The egg found in an abandoned nest is not an accurate clutch size, because we do not know if the clutch had been completed, or had undergone brood reduction. This egg was white, without spots (as egg fragments found at N1). This color pattern is not typical for *Buteo* eggs, which have been described as generally spotted or blotched, on a white or whitish background (Brown and Amadon 1968). However, in some species, as Galápagos (*B. galapagoensis*), Zone-tailed (*B. albonotatus*), and Gurney's (*B. poecilochrous*) hawks, eggs are described as white and unmarked (Brown and Amadon 1968).

Most *Buteo* species nest in trees, but, in certain cases, they also can use cliff ledges or bushes when trees are not available. Occasionally, human structures (e.g., power poles) and nests constructed by other birds (or even squirrels) have been reported as nesting substrates (del Hoyo et al. 1994). Even ground nesting has been observed for the Swainson's Hawk (*B. swainsoni*); (Woffinden and Mosher 1977). All nests we found of the White-throated Hawk were constructed in large southern beech trees, including nests in semi-urban habitats (Gelain et al. 2001). This use of high *Nothofagus* trees was also noted by Pavez (2000) in central Chile. Outside the austral temperate forests of southern Chile and Argentina, there is no information on the nesting biology of this species. Even its breeding distribution and migratory status remain unknown (del Hoyo et al. 1994, Ferguson-Lees and Christie 2001). Consequently, the capability of this species to use other kinds of substrates for nesting is unknown. There is a single report of nesting on a rocky promontory in northern Chile (Goodall et al. 1957, Johnson 1965), but given the characteristics reported, it is unclear if the species was identified correctly.

Almost all *Buteo* hawks line their nests with greenery (del Hoyo et al. 1994). When trees are not available or scarce, hawks use grass, feathers, sedges, moss, small roots, wool, bark, hair, cow or horse dung (del Hoyo et al. 1994). The use of green plant material in bird nests has been suggested to help minimize the harmful effects of ectoparasites (Wimberger 1984), to keep the chicks

above the excreta and food remains that are dropped in the nest bowl (Snyder 1975), or as an advertisement to other aerial raptors that the nest is occupied (Newton 1979).

Although the White-throated Hawk appears to be a more abundant raptor than historically reported in Patagonia (Casas and Gelain 1995, Trejo et al. 2001, Gelain et al. 2001), and seems to be rather tolerant to humans during breeding (Gelain et al. 2001), further information is needed on its habitat requirements. Increasing forest loss in Patagonia may negatively affect this species, especially if these forests comprise its primary breeding area.

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NESTLING PROVISIONING RATES OF PEREGRINE FALCONS IN INTERIOR ALASKA

ANGELA G. PALMER,¹ DANA L. NORDMEYER,² AND DANIEL D. ROBY

USGS—Oregon Cooperative Fish and Wildlife Research Unit and Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, OR 97331 U.S.A.

ABSTRACT.—We examined factors influencing nestling provisioning rates among Peregrine Falcons (*Falco peregrinus*) breeding along the Tanana River, Alaska, in 1995–97. Perching birds (Passeriformes) composed the majority (54.3%) of prey delivered to the nests; whereas, ducks and grebes composed the majority of prey biomass (60.8%). After accounting for stage of the nesting cycle, delivery rates of prey items and estimated prey mass increased with brood size. Prey mass was positively correlated with the length of time an adult was absent from the vicinity of the nest prior to prey delivery. Finally, although we found that delivery rates of prey per nestling decreased with increasing brood size, estimated mass delivered per nestling did not vary with brood size. Peregrine Falcons apparently maintained constant provisioning rates per nestling as brood size increased by increasing prey mass.

KEY WORDS: *Peregrine Falcon; Falco peregrinus; foraging theory; Interior Alaska; nestling diet; nestling provisioning rates.*

TASAS DE APROVISIONAMIENTO A LOS POLLUELOS EN LOS HALCONES PEREGRINOS DEL INTERIOR DE ALASKA

RESUMEN.—Examinamos los factores que influencian las tasas de aprovisionamiento entre halcones peregrinos (*Falco peregrinus*) que se reprodujeron a lo largo del río Tanana, Alaska, en 1995–97. Los pájaros (Passeriformes) componen la mayoría (54.3%) de las presas entregadas en los nidos; mientras que, los patos y los zambullidores comprenden la mayoría de la biomasa de las presas (60.8%). Después de dar cuenta de la etapa del ciclo de anidamiento, las tasas de entrega de los ítem presa y la masa estimada de las presas incrementa con el tamaño de la nidada. La masa de la presa estuvo correlacionada positivamente con la longitud del tiempo en la que el adulto estuvo ausente de la vecindad del nido antes de la entrega de la presa. Finalmente, aunque encontramos que la tasa de entrega de presa por polluelo decreció con el aumento del tamaño de la nidada, la estimación de la masa entregada por polluelo no varió con el tamaño de la nidada. Los halcones peregrinos aparentemente mantuvieron constantes las tasas de aprovisionamiento por polluelo en nidadas que incrementaron su tamaño por medio del aumento del tamaño de las presas.

[Traducción de César Márquez]

Parent birds must provision nestlings adequately to ensure growth and survival of nidicolous young. Parents are limited in their ability to provide for nestlings by both environmental conditions and physiological constraints (Newton 1986), and parents confront a trade-off between investing in present versus future reproduction (Trivers 1972). Deerenberg et al. (1995) supported the existence of a trade-off between present and future reproduc-

tion by showing that daily energy expenditure of breeding Eurasian Kestrels (*Falco tinnunculus*) increased with artificially enhanced brood size, and was negatively correlated with subsequent survival of parents. In addition, although parents raising larger broods contribute more offspring to the population, the fitness of each fledgling from large broods may be lower than the fitness of fledglings from smaller broods (Dijkstra et al. 1990).

Lack (1954) and Gibb (1955) proposed that parent birds work as hard as they can to feed young, and that chicks from relatively larger broods are fed less than nestlings in average-sized broods. According to their hypothesis, provisioning rates per nestling should decline with a convex function as

¹ Present address: ABR, Inc., Environmental Research and Services, P.O. Box 240268, Anchorage, AK 99524 U.S.A.; e-mail address: apalmer@abrincc.com

² Present address: 5073 C Polaris Street, Eielson Air Force Base, AK 99702 U.S.A.

brood size increases. A survey of the literature on feeding frequencies of nestlings indicated that concave declines in feeding frequencies per nestling with increasing brood size are the norm, at least among passerines (Nur 1987). Among raptors, Newton (1986) found Eurasian Sparrowhawk (*Accipiter nisus*) prey-delivery rates were not influenced by the number of young in the nest; however, Masman et al. (1988) observed that male Eurasian Kestrels responded to experimentally increased hunger of broods by increasing active hunting.

Few studies have examined raptor provisioning rates and their relation to brood size. Enderson et al. (1972) found that larger Peregrine Falcon (*Falco peregrinus*) broods in Interior Alaska were fed more often, but individual nestlings in large broods received fewer feedings than small broods ($N = 7$ broods). White and Nelson (1991) documented the prey-delivery rate of one male peregrine to be approximately one prey item per hour. At 13 Peregrine Falcon nests in Australia, Olsen et al. (1998) observed that males provided more prey deliveries and more biomass to large broods than to broods of one or two chicks. We examined the relationships among Peregrine Falcon prey-delivery rate, prey size, mass-delivery rate, and brood size.

If Peregrine Falcon pairs were flexible in how they met food requirements of nestlings, we expected to find differences among pairs in prey-delivery rates and prey size in relation to brood size. We anticipated that mass-delivery rates (g/hr), a function of prey-delivery rates (items/hr) and prey size (g/item), would increase with increasing brood size.

Peregrine Falcons select a wide variety of predominantly avian prey species and sizes, and hunt over large local geographical areas (White and Nelson 1991, Ratcliffe 1993, Enderson and Craig 1997). They are thus good subjects for examining relationships between prey size and foraging time. We examined correlations between time away from the nest prior to a delivery and size of prey delivered.

Raising larger broods can produce more fledglings, but can be more energetically costly for parents (Deerenberg et al. 1995). We expected parents to deliver more food to larger broods, but because of the energetic costs of provisioning, pairs with larger broods would not be expected to provide as much food per nestling as pairs with smaller broods. Alternatively, if parents fully com-

pensated for each additional nestling in a brood, or if parents of higher individual quality produce larger broods, we would expect provisioning rates per nestling to be similar, regardless of brood size.

METHODS

Study Area. The study area encompassed a 250-km stretch of the Tanana River between Tok and Fairbanks, Alaska (from $63^{\circ}8'N$, $143^{\circ}36'W$ – $64^{\circ}18'N$, $148^{\circ}45'W$). In 1995, the study area extended from Tanacross to Sawmill, a 110-km stretch of river. In 1996 and 1997, we included an additional 65-km section of the river from Delta to Salcha. Observations were initiated each year after ice break-up in mid-May, and continued until the young had fledged and left the area of the nest in late-August to early-September. Two separate crews of 2–4 observers recorded data at nests.

Nests, which were situated on bluffs overlooking the river, were selected based on availability of accessible observation sites on gravel bars opposite cliffs with visibility of the nest ledge. To observe prey deliveries we established sites across at least one channel of the river and about 300 m from nests.

Provisioning Rates. Each field crew used binoculars, 15–60× spotting scopes, and a 90× Questar® (New Hope, PA) telescope to assist with observations. We kept the Questar trained on the nestlings or fledglings to aid our identification of prey deliveries. During the brood-rearing period, at least two (1995) or three (1996–97) observers recorded data. In all years, at least four observers recorded data during the post-fledging stage of the nesting cycle. Observations were performed during daylight hours.

We observed 10 breeding pairs in 1995, 9 breeding pairs in 1996, and 10 breeding pairs in 1997 from a total of 17 nest sites, where a nest site was defined as a nesting territory with a breeding pair (Steenhof 1987). Of these sites, we observed eight sites in one year only, six sites in two years, and three sites during all three years of the study. We made observations during the brood-rearing and post-fledging phases. Of the 10 breeding pairs observed in 1995, we observed all during brood-rearing and four during post-fledging periods. In 1996, we recorded provisioning rates from eight breeding pairs during brood-rearing period. One nest failed prior to fledging, we observed provisioning rates from the seven remaining pairs plus an additional pair during the post-fledging stage. In 1997, we observed all 10 breeding pairs during both brood-rearing and post-fledging. For analysis, we subdivided observations into four stages of the nesting cycle: early brood-rearing periods (0–10 d post-hatch), mid-brood-rearing (11–24 d), late brood-rearing (25 d until fledging), and post-fledging (ca. 40+ d) stages. We determined the stages of the brood-rearing phase during banding visits by estimating age of the oldest chick based on feather development and comparisons to Nelson's (1970) drawings of chicks. During early, mid, and late brood-rearing, and post-fledging stages, we made observations from 12, 14, 18, and 22 breeding pairs respectively (all years combined; Table 1).

For each breeding pair, we recorded the number of prey deliveries, the estimated size class of each prey item,

Table 1. Number of breeding Peregrine Falcon pairs observed by brood size during each stage of the nesting cycle along the Tanana River, Alaska 1995–97.

STAGE OF THE BREEDING CYCLE	BROOD SIZE				TOTAL
	1	2	3	4	
Early nestling-rearing	2 (9) ^a	2 (10)	5 (23)	3 (11)	12
Mid nestling-rearing	1 (5)	5 (29)	4 (15)	4 (17)	14
Late nestling-rearing	3 (6)	5 (23)	8 (27)	2 (8)	18
Post-fledging	4 (15)	9 (45)	5 (22)	4 (19)	22

^a (Total number of 4-hr observation sessions).

and the type of prey delivered (identified to finest taxon possible). To measure provisioning rates, we estimated the mass of those prey identified to species using mean body mass of that species (Burt and Grossenheider 1980, Dunning 1993). For prey identified only to genus or family, we used the mean mass of all the species of that genus or family (Dunning 1993) that regularly occurred in the study area, except in the case of shorebirds, which span a wide range of masses. We classified shorebirds and prey not identified to species, genus, or family into the following size classes: small (9–50 g), medium (51–200 g), large (201+ g), or unknown, to assign them an estimated mass. For both shorebirds and prey identified only to size-class, we used the median mass of all species of that size class known to regularly occur in the study area (30 g, 125 g, and 641 g for small, medium, and large items, respectively). We categorized prey of unknown size-class as medium-sized prey.

Peregrines sometimes delivered, cached, and redelivered prey items several times. In these instances, we counted the item as a single prey delivery. If part of a carcass (identified to species, genus, or family) was delivered, we assigned it the mass of that species, genus, or family, as outlined above. For unidentified partial carcasses we estimated the size of that item in relation to the size of the adult falcon and assigned it a size class of small (9–50 g), medium (51–200 g), or large (201+ g), based on the above methods of mass assignments.

For categorical analysis of prey size in relation to brood size, we only included those prey identified to species, genus or family, and classified items in small, medium, or large classes, based on the above methods of mass assignments.

Two video cameras, equipped with 250 mm lenses and 2× extenders, were employed to record prey deliveries continuously during observation sessions from observation sites. In 1995, we used Canon L2 Hi-8 mm (Canon, Inc., Tokyo, Japan) and Sony CCD-FX430 8 mm video cameras (Sony Corporation, Tokyo, Japan), and in 1996 and 1997 we used Canon L2 cameras. During the brood-rearing stage, one camera was focused on the nest ledge, while the other was focused on the attending adult. During the post-fledging stage, we focused on fledglings or adults as visibility allowed. Videotapes confirmed prey deliveries if observations were uncertain.

We estimated mass-delivery rates during each stage of the nesting cycle for each nest by averaging total mass delivered among 4-hr observation sessions. Similarly, we

calculated prey-delivery rates during each stage for each nest by averaging total number of prey delivered during 4-hr observation sessions. Finally, to estimate mean mass per session per nest per stage, we divided the total estimated mass of prey delivered by the total number of items delivered per 4-hr observation session, and then calculated the mean for the total number of observation sessions in that stage. During a given stage of the nesting cycle we conducted a mean of 4.0 (SD = 2.4) 4-hr observation sessions at a given nest, with a total of 284 observation sessions at all nests (Table 1). Observation sessions were sometimes back-to-back. We sampled provisioning rates from all daylight hours at each nest during each stage of the nesting cycle observed; however, observations at all nests were concentrated from 0800–1700 H Alaska Daylight Time. Observation sessions were excluded from analyses if poor visibility persisted throughout the session or, in the case of the post-fledging stage, when fledglings were not at the nest site. We treated nest sites independently among years.

We also examined the relationship between the length of time an adult was absent from the vicinity of the nest prior to a delivery (time away) and the estimated mass of the prey delivered. For this analysis, we excluded the first item of every observation session and included only prey identified to species, genus, or family.

For successful nests, mean brood size at fledging was 2.55 (SD = 1.0, range = 1–4 nestlings; Nordmeyer 1999), which was similar to mean brood size reported throughout Interior Alaska (Cade 1960, Ambrose et al. 1988, J Wright and P. Bente unpubl. data). Five nests had one chick, nine nests had two chicks, nine nests had three chicks, and six nests had four chicks. We observed four nests that experienced reductions in brood size prior to fledging: two broods from three to one chick, one brood from three to two chicks, and the fourth brood from four to three chicks.

Statistical Analyses. We used linear regression to assess the relationships of estimated number and mass of prey delivered and mean estimated prey mass as a function of brood size, and of estimated mass as a function of time away. We used Analysis of Variance (ANOVA) and Bonferroni's multiple comparison procedure to assess differences in provisioning rates among stages of the nesting period. We used lack-of-fit *F*-tests to test the adequacy of linear regression models versus separate means models for comparisons between provisioning rates and brood size. In the regression analyses we accounted for stage of

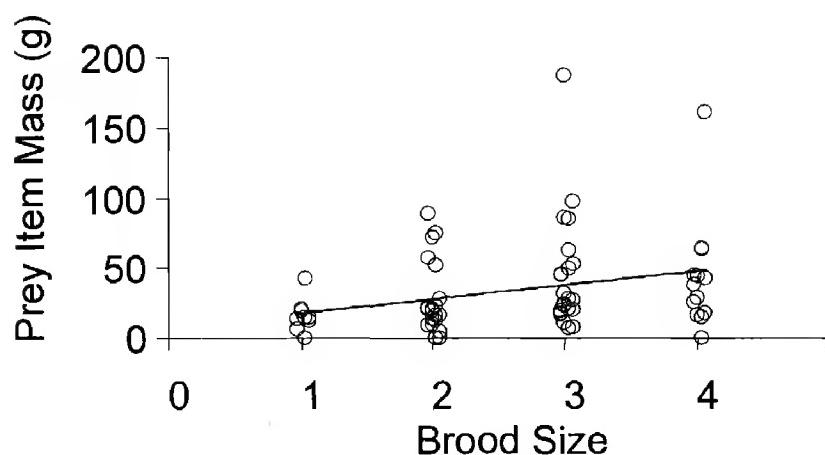


Figure 1. The relationship between prey item mass and brood size among Peregrine Falcons breeding along the Tanana River, Alaska, 1995–97. Prey item mass is presented as mean estimated prey item mass per nest per stage of the nesting period. The regression line is not adjusted for stage of the nesting period.

the nesting period and used weighted means based on the sample size of 4-hr observation blocks from each nest per stage, but we present unadjusted data in the figures. We log-transformed mass-delivery rates to meet the assumptions of the statistical tests. Additionally, we used a χ^2 test to examine the relationship between prey size-class and brood size. Means are reported as $\bar{x} \pm \text{SE}$.

RESULTS

Taxonomic Composition of Prey. Of the 343 prey observed delivered to nestlings, 201 (58.6%) could be identified to a taxonomic group. Most identified prey were passerines (Passeriformes; 54.3%), with shorebirds (Charadriiformes; 23.5%), ducks (Anatidae) and grebes (Podicipedidae; 13.0%), and gulls and terns (Laridae; 6.5%) comprising most of the remainder (Table 2). Ducks and grebes were the most important prey category in terms of biomass, comprising 60.8% of total estimated prey biomass. Shorebirds followed at 14.1%, gulls and terns at 9.7%, and passerines at 11.2% of total prey biomass. Small mammals were delivered on three occasions, and comprised an estimated 1.1% of prey biomass.

Prey Size. Of the 343 prey that we observed being delivered to young, 232 items (67.6%) were identified to a size category. Overall, more small items (126; 54.3%) were delivered than either medium (69; 29.7%) or large (37; 15.9%) items (χ^2_2 goodness of fit test = 52, $P < 0.001$). When prey of all size-categories were included, there was a trend towards a relationship between brood size and prey size class (χ^2_6 contingency test for independence = 11.14, $P = 0.08$), indicating that in general, parents with small broods deliver smaller items than parents with large broods. Additionally,

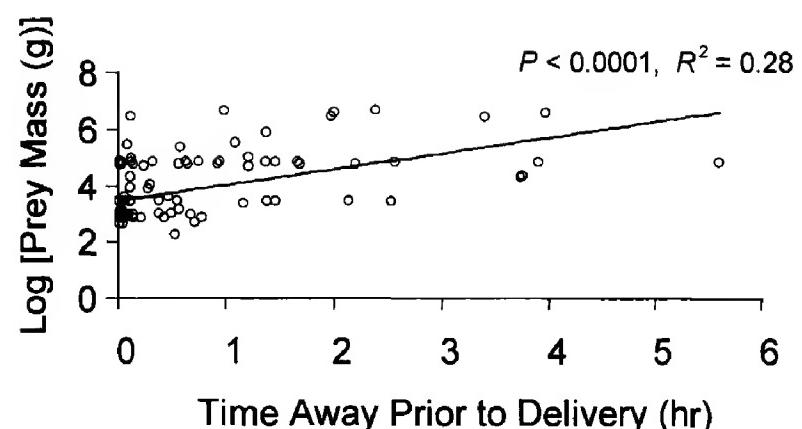
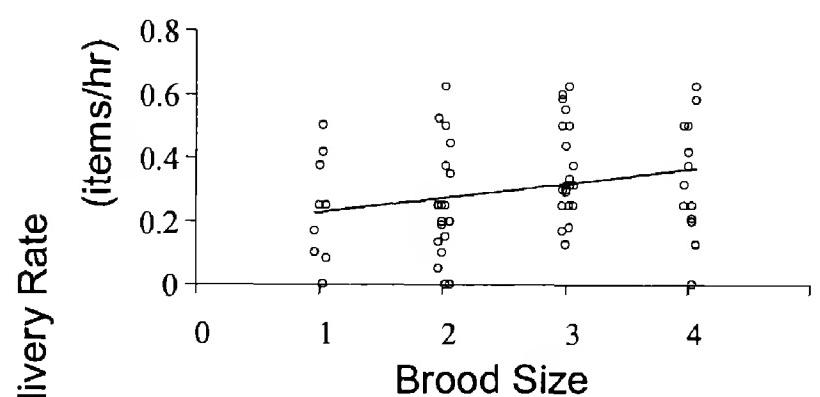


Figure 2. Log (estimated prey mass) as a function of time away from nest cliff prior to prey delivery for Peregrine Falcons nesting along the Tanana River, Alaska, 1995–97.

we noted a trend towards fewer medium-sized items brought to broods of two ($P = 0.11$, analysis of standardized residuals).

We found a positive relationship between prey mass and brood size ($P < 0.05$, $R^2 = 0.15$, $N = 66$). Median prey mass increased a mean of 24% ($\pm 10\%$) with each additional nestling (Fig. 1). Par-

a. Per Brood



b. Per Nestling

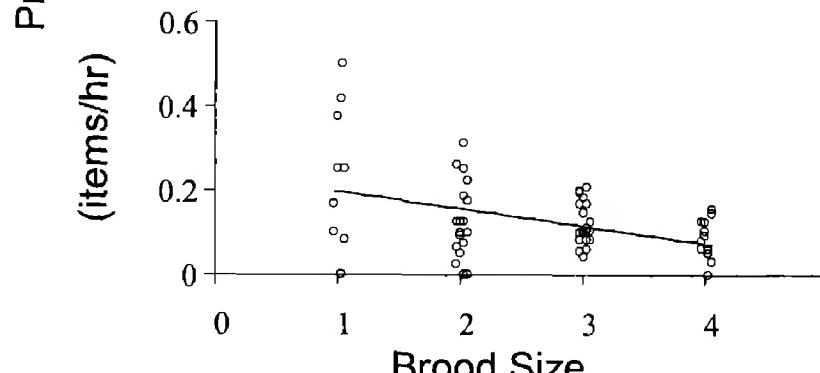


Figure 3. Mean prey delivery rates per brood (a) and per nestling (b) as a function of brood size in Peregrine Falcons nesting along the Tanana River, Alaska, 1995–97. The regression lines are not adjusted for stage of the nesting period.

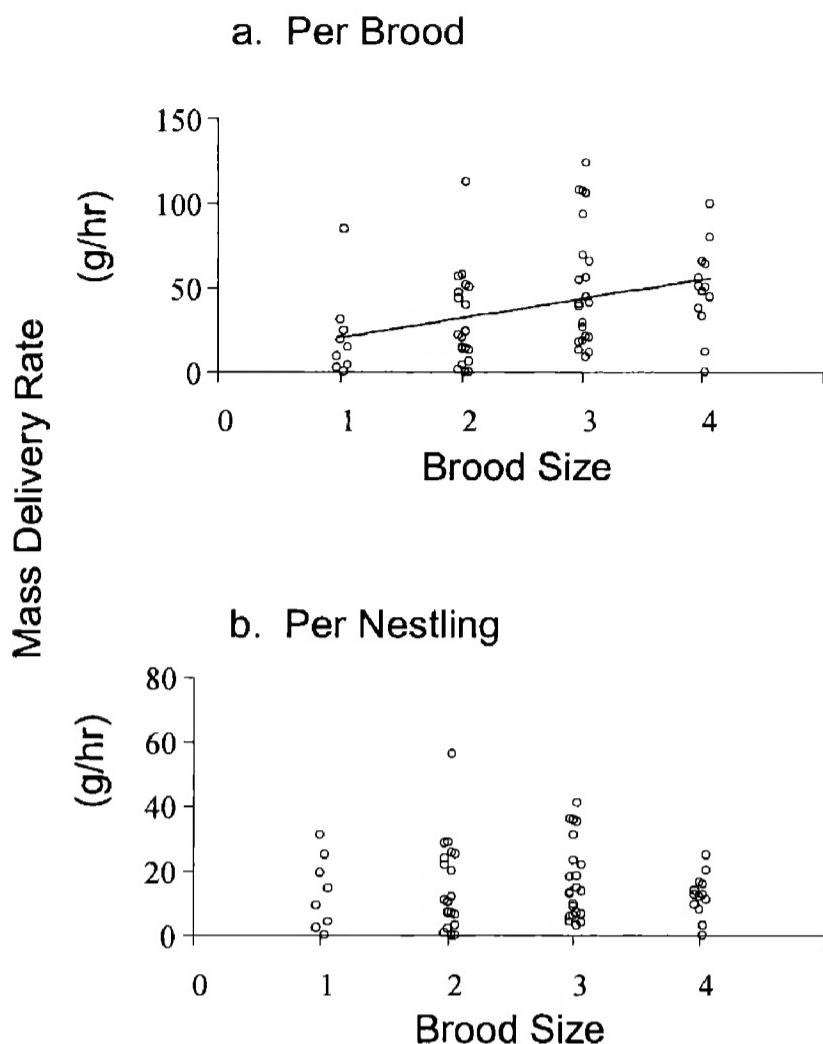


Figure 4. Mass-delivery rate per brood (a) and per nestling (b) as a function of brood size in Peregrine Falcons nesting along the Tanana River, Alaska, 1995–97. In (a) the regression line is not adjusted for stage of the nesting period. In (b) no linear relationship was evident per nestling.

ents of single-chick broods delivered no prey over 200 g, during 140 hr of obervations and 31 deliveries, except for one delivery of a gull (*Larus* spp.; 308 g). Together with data on prey size, these analyses indicate that Peregrine Falcons maintained provisioning rates for larger broods by increasing mean prey size.

Time Away. There was a positive relationship between the time an adult was away from the nest area prior to a prey delivery (hr) and estimated mass of delivered prey (slope = 0.51 [log(g) hr⁻¹] ± 0.08, $P < 0.001$, $R^2 = 0.29$, $N = 111$; Fig. 2). This is consistent with the inverse relationship between number of prey delivered and mean mass (slope = -2.09 ± 0.27, $P < 0.001$, $R^2 = 65.8$, $N = 66$).

Stage of the Nesting Cycle and Prey-provisioning Rates. Prey-delivery rates did not differ among stages of the nesting period ($N = 66$, $P > 0.10$ for family-wise multiple comparisons). Prey mass and mass-delivery rates also did not differ among stages

of the nesting period ($F_{3,65} = 1.04$, $P > 0.3$; and $F_{3,65} = 1.19$, $P > 0.3$; respectively).

Brood Size and Prey-provisioning Rates. Brood size was positively related with both prey-delivery rate ($R^2 = 0.35$, $P = 0.002$, $N = 66$; Fig. 3a) and mass-delivery rate ($R^2 = 0.25$, $P = 0.02$, $N = 66$; Fig. 4a). Supporting these relationships, a positive linear relationship was suggested between both prey-delivery rates and mass-delivery rate versus brood size, (Lack-of-Fit F -tests were not significant: $P = 0.93$ and $P = 0.71$, respectively). Peregrine Falcons delivered a mean of 23% ($\pm 7\%$) more prey with each additional chick in the brood, and median mass-delivery rates increased 53% ($\pm 12\%$) with each additional chick.

Prey Provisioning Per Nestling. Prey-delivery rates per nestling declined with increasing brood size ($P = 0.001$, $R^2 = 37.7$, $N = 66$; Fig. 3b). In contrast, mass-delivery rates per nestling did not change appreciably with increasing brood size (Fig. 4b). Median prey-delivery rate per nestling declined 8% ($\pm 6\%$; Fig. 3b) with each additional nestling. In contrast, the slope of the regression of mass delivery rate per nestling on brood size did not differ from zero, after accounting for nesting stage (2-sided test, $P > 0.5$; Fig. 4b). This suggests that breeding pairs did not compensate for larger broods by proportionately increasing the rate of prey delivery, but instead increased the size of prey delivered.

DISCUSSION

Our results are consistent with the hypothesis that parents must work harder to provide for larger broods. Pairs with larger broods had higher prey-delivery rates (Fig. 3a), and higher mass-delivery rates (Fig. 4a). However, prey-delivery rates per nestling declined with increasing brood size, indicating that, by capturing proportionately more prey, parents did not fully compensate for larger broods (Fig. 3b). Additionally, we found no relationship between per nestling mass-delivery rates and brood size; the mass-delivery rate was constant across brood sizes (Fig. 4b). Prey-delivery rates per nestling declined with increasing brood sizes. Thus, to maintain constant mass-delivery rates per nestling across brood sizes, parents of larger broods must have compensated for lower prey-delivery rates per nestling by providing larger prey on average. In support of this interpretation, prey mass increased with brood size (Fig. 1), and parents of small broods rarely delivered large items.

Table 2. Frequencies of prey items observed and identified upon delivery to Peregrine Falcon nestlings at nests along the Tanana River, Alaska 1995–97

COMMON NAME (SCIENTIFIC NAME)	AGE/SEX	FREQUENCY	PERCENT OCCURRENCE	BODY MASS (g) ^a	PERCENT TOTAL PREY MASS
Grebe spp. (Red-necked or Horned) (<i>Podiceps</i> spp.)	—	3	1.5	738	8.3
Mallard (<i>Anas platyrhynchos</i>)	female	2	1.0	1082	8.1
American Wigeon (<i>Anas americana</i>)	female	1	0.5	719	2.7
American Wigeon (<i>Anas americana</i>)	male	2	1.0	792	6.0
Green-winged Teal (<i>Anas crecca</i>)	male	1	0.5	364	1.4
Green-winged Teal (<i>Anas crecca</i>)	—	2	1.0	340	2.6
Scaup spp. (Greater or Lesser) (<i>Aythya</i> spp.)	male	1	0.5	891	3.3
Duck spp. (Anatinae spp.)	female	1	0.5	722	2.7
Duck spp. (Anatinae spp.)	—	6	3.0	746	16.8
Duckling (Anatinae spp.)	Juvenile	4	2.0	30	0.5
Duck/grebe spp. (Anatinae spp. or <i>Podiceps</i> spp.)	—	3	1.5	745	8.4
Total ducks and grebes (Anatinae and Podicipedidae)	—	26	13.0	60.8	
Red-necked Phalarope (<i>Phalaropus lobatus</i>)	—	1	0.5	34	0.1
Least Sandpiper (<i>Calidris minutilla</i>)	—	2	1.0	23	0.2
Lesser Yellowlegs (<i>Tringa flavipes</i>)	—	7	3.5	81	2.1
Yellowlegs spp. (Greater or Lesser) (<i>T. flavipes</i> or <i>T. melanoleuca</i>)	—	5	2.5	126	2.4
Solitary Sandpiper (<i>Tringa solitaria</i>)	Juvenile	1	0.5	48	0.2
Upland Sandpiper (<i>Bartramia longicauda</i>)	—	1	0.5	150	0.6
Spotted Sandpiper (<i>Actitis macularia</i>)	—	10	5.0	32	1.2
Spotted Sandpiper (<i>Actitis macularia</i>)	—	3	1.5	32	0.4
Shorebird spp. (Scolopacidae spp.) small	Juvenile	3	1.5	30	0.3
Shorebird spp. (Scolopacidae spp.) medium	—	14	7.0	125	6.6
Total Shorebirds (Scolopacidae)	—	47	23.5	14.1	
Mew Gull (<i>Larus canus</i>)	—	1	0.5	404	1.5
Bonaparte's Gull (<i>Larus philadelphia</i>)	—	1	0.5	212	0.8
Gull spp. (Mew or Bonaparte's (<i>Larus</i> spp.))	—	3	1.5	308	3.5
Gull nestling (<i>Larus</i> spp.)	Juvenile	2	1.0	125	0.9
Arctic Tern (<i>Sterna paradisaea</i>)	—	5	2.5	110	2.1
Gull/tern spp. (<i>Larus</i> spp. or <i>Sterna</i> spp.)	—	1	0.5	242	0.9
Total gulls and terns (Laridae or Sternidae)	—	13	6.5	9.7	
Rock Dove (<i>Columba livia</i>)	—	1	0.5	355	1.3
Northern Flicker (<i>Colaptes auratus</i>)	—	1	0.5	142	0.5
Grouse spp. (<i>Bonasa umbellus</i> or <i>Dendragapus canadensis</i>)	—	1	0.5	337	1.3

Table 2. Continued.

COMMON NAME (SCIENTIFIC NAME)	AGE/SEX	FREQUENCY	PERCENT OCCURRENCE	BODY MASS (g) ^a	PERCENT TOTAL PREY MASS
Olive-sided Flycatcher (<i>Contopus cooperi</i>)	—	1	0.5	32	0.1
Bohemian Waxwing (<i>Bombycilla garrulus</i>)	—	1	0.5	56	0.2
Black-billed Magpie (<i>Pica pica</i>)	—	2	1.0	178	1.3
Gray Jay (<i>Perisoreus canadensis</i>)	—	4	2.0	73	1.1
Gray Jay (<i>Perisoreus canadensis</i>)	Juvenile	1	0.5	73	0.3
Dark-eyed Junco (<i>Junco hyemalis</i>)	—	8	4.0	20	0.6
Cliff Swallow (<i>Petrochelidon pyrrhonota</i>)	—	1	0.5	22	0.1
Violet-green Swallow (<i>Tachycineta thalassina</i>)	—	6	3.0	14	0.3
Violet-green Swallow (<i>Tachycineta thalassina</i>)	Juvenile	1	0.5	14	0.1
Bank Swallow (<i>Riparia riparia</i>)	—	2	1.0	15	0.1
Tree Swallow/Violet-green Swallow (<i>T. bicolor</i> or <i>T. thalassina</i>)	—	45	22.4	18	3.0
Swallow spp. (Cliff, Tree, Violet-green, or Bank) (Hirundinidae)	Juvenile	6	3.0	18	0.4
Swallow spp. (Hirundinidae spp.)	—	1	0.5	10	0.1
Yellow Warbler (<i>Dendroica petechia</i>)	—	2	1.0	11	0.1
Black-capped Chickadee (<i>Poecile atricapillus</i>)	—	1	0.5	34	0.1
Townsend's Solitaire (<i>Myadestes townsendi</i>)	—	1	0.5	31	0.1
Swainson's Thrush (<i>Catharus ustulatus</i>)	—	1	0.5	77	0.3
Varied Thrush (<i>Ixoreus naevius</i>)	—	1	0.5	77	0.3
American Robin (<i>Turdus migratorius</i>)	—	1	0.5	32	0.1
Thrush spp. (Gray-cheeked, Swainson's, or Hermit) (<i>Catharus</i> spp.)	—	1	0.5	30	2.5
Small passerine spp. (Passeriformes spp.)	—	22	10.9	54.3	11.2
Total perching birds (Passeriformes)	—	109	—	—	—
Unknown avian spp.	—	142	—	—	—
Red Squirrel (<i>Tamiasciurus hudsonicus</i>)	—	1	0.5	240	0.9
Small rodent (Rodentia)	—	2	1.0	30	0.2
Total small mammal	—	3	1.5	1.1	1.1
Total	(343)	201 = 100%	26 616	g = 100%	

^a We estimated prey mass using the mean body mass of that species (Dunning 1993). For prey identified to genus or family, we used the mean mass of all the species of that genus or family (Dunning 1993) that regularly occur in the study area, except in the case of shorebirds, which span a wide range of masses. We classified shorebirds into small (9–50 g) or medium (51–200 g) size classes based on estimated size in the field and assigned them the median mass of all species of that size class known to regularly occur in the study area (30 g and 125 g, respectively). We estimated mammalian prey masses from Burt and Grossenheimer (1980).

Thus, different brood sizes seemed to be associated with different parental foraging strategies.

Time away from the nest prior to a delivery and size of prey were positively correlated (Fig. 2). Several variables can affect the time required for successful capture and delivery of prey of various sizes, such as hunger level of brood (Tinbergen and Drent 1980, Steidl and Anthony 2000), prey availability and distribution (Hunter et al. 1988, Meese and Fuller 1989, Rosenfield et al. 1995, Hakkarainen et al. 1997), prey handling time (Beissinger 1983), foraging efficiency (Winkler and Allen 1995, Bennetts and McClelland 1997), weather conditions (Steidl 1995), or distance traveled from the nest (Schoener 1979).

Cost of reproduction theory suggests that raising the maximum possible number of young causes reductions in parental survival, and thus, natural brood sizes are lower than maximum to optimize future survival and maximize lifetime reproductive output of adults (Dijkstra et al. 1990). Indeed, Nelson's (1988) observation that Peregrine Falcons more often failed to return to nest territories after rearing broods of three or four than after rearing broods of zero to two chicks suggests a cost to adults of raising larger broods. Also, Deerenberg et al. (1995) demonstrated a direct relationship between increased individual work-rate in parents with experimentally enlarged broods and local survival rate among adult Eurasian Kestrels. They proposed that an optimal work-rate might be a proximate control mechanism for brood size, because high work-rates may entail physiological weakening, leading to lower survival rates of breeders. Tolonen and Korpimäki (1996) suggest that parental effort (time spent flight hunting/total time) among Eurasian Kestrels is adjusted to the level where parental survival is not jeopardized, based on their evidence that males did not change parental effort in response to brood size manipulation, and females made only minor changes.

Mass-delivery rates per nestling, unlike per nestling prey-delivery rates, were constant across the range of brood sizes observed in this study. One possible explanation for constant mass-delivery rates per nestling, regardless of brood size, is that parents of smaller broods were working far below maximum sustained working capacity (Dijkstra et al. 1990, Stearns 1992). This could be because prey were readily available and easy to acquire. An alternative explanation is that pairs with larger

broods were better providers and able to regularly kill larger prey and transport it to the nest.

To raise large broods, parents must be efficient hunters to capture and deliver prey at adequate provisioning rates, and they need to maintain a work rate that does not impinge excessively on their future survival, and thus, reduce lifetime reproductive output (Deerenberg et al. 1995). If natural brood size is an indication of optimal workload per pair, then brood size may reflect parental foraging efficiency. In general, we observed more prey and larger prey delivered to larger broods. Larger prey were related to longer periods away from the nest area prior to delivery. In natural broods, we found parents had equal mass-delivery rates per nestling regardless of brood size, presumably maximizing both their present and future reproductive output. In our study, we were not able to evaluate the influence of age and breeding experience, which could be important factors on brood size and provisioning patterns. In future studies, distinguishing between parental hunting efficiency and prey availability will be essential to test foraging theory as it relates to provisioning of Peregrine Falcon young.

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PERCH SITES AND HUNTING BEHAVIOR OF RED-TAILED HAWKS (*BUTEO JAMAICENSIS*)

JENNIFER E. LEYHE AND GARY RITCHISON¹

Department of Biological Sciences, Eastern Kentucky University, Richmond, KY 40475 U.S.A.

ABSTRACT.—For sit-and-wait predators like Red-tailed Hawks (*Buteo jamaicensis*), perch sites are important components of hunting ranges. From October 1999–July 2000, perches ($N = 270$) used by Red-tailed Hawks in central Kentucky were located and characterized. Perches used by Red-tailed Hawks were relatively high ($\bar{x} = 12.3$ m) in trees or on poles. Such perches provide a large, relatively unobstructed field of view and likely increase the chances of detecting prey. Red-tailed Hawks spent more time on perches before attacking than before giving up, perhaps waiting to attack prey after locating it to increase the chance of a successful attack. Characteristics of vegetation around perches used by hunting Red-tailed Hawks differed from those of areas around available (but apparently unused) sites during both the breeding and nonbreeding seasons. During the breeding season, areas used by Red-tailed Hawks had less forb cover, lower vegetation density, and shorter vegetation than available areas. During the nonbreeding season, areas used by Red-tailed Hawks were characterized by less bare ground, more grass cover, less shrub cover, fewer small trees, decreased vegetation density, and shorter vegetation than available areas. In general, used areas provided less cover, which may increase prey vulnerability.

KEY WORDS: *Red-tailed Hawk; Buteo jamaicensis; giving-up time; hunting; perch site.*

SITIOS DE PERCHA Y COMPORTAMIENTO DE CAZA DE LOS GAVILANES DE COLA ROJA (*BUTEO JAMAICENSIS*)

RESUMEN.—Para los depredadores que se perchan a esperar sus presas como el gavilán de cola roja (*Buteo jamaicensis*), los sitios de percha son componentes importantes de sus rangos de caza. Desde octubre de 1999 a Julio 2000, se localizaron y caracterizaron las perchas ($N = 270$) usadas por los gavilanes de cola roja en Kentucky central. Las perchas usadas por los gavilanes de cola roja fueron relativamente altas ($\bar{x} = 12.3$ m) en árboles o en postes. Tales perchas proveen un gran y relativamente no obstruido campo de vista y probablemente incrementan la probabilidad de detectar las presas. Los gavilanes de cola roja pasan mas tiempo en las perchas antes de atacar que antes de desistir, esperando quizás atacar las presas después de localizarlas para incrementar la probabilidad de un ataque exitoso. Las características de la vegetación alrededor de las perchas usadas por este gavilán para cazar, difirieron de aquellas áreas alrededor de sitios disponibles (y aparentemente sin uso) tanto durante la temporada reproductiva como no reproductiva. Durante la temporada reproductiva las áreas usadas por el gavilán de cola roja tenían menor cobertura de horquetas, una densidad de vegetación más baja, y vegetación más baja que en las áreas disponibles. Durante la temporada no reproductiva, las áreas usadas por los gavilanes se caracterizaron por un suelo menos desnudo, mayor cobertura de pastos, menor cobertura de arbustos, árboles pequeños más escasos, decrecimiento en la densidad de la vegetación y vegetación más corta que en las áreas disponibles. En general, las áreas usadas tenian menos cobertura, lo cual puede incrementar la vulnerabilidad de las presas.

[Traducción de César Márquez]

Red-tailed Hawks (*Buteo jamaicensis*) generally inhabit open areas with scattered trees used as hunting and roosting sites (Preston and Beane 1993). Perch sites are important components of Red-tailed Hawk territories (Fitch et al. 1946) because

they are sit-and-wait predators (Craighead and Craighead 1956). Red-tailed hawks and other raptors may prefer certain perches over others (Fitch et al. 1946). For example, Bohall and Collopy (1984) found that both Red-tailed and Red-shouldered hawks (*Buteo lineatus*) preferred natural perches, mainly snags and bare trees, over man-made perches. In the autumn, Chamberlin (1974)

¹ Corresponding author's e-mail address: gary.ritchison@eku.edu

reported that Red-tailed Hawks preferred to hunt from isolated trees at a height of 12.5–18.3 m. During the summer, Red-tailed Hawks may prefer lower perches that provide some shade (Fitch et al. 1946).

Despite the importance of perches, few investigators (Fitch et al. 1946, Chamberlin 1974, Bohall and Collopy 1984) have described perch site selection by Red-tailed Hawks. Little is known about the features of perches chosen by these hawks or the characteristics of used versus available perches. In addition, possible differences in the hunting behavior of these hawks among or between seasons have not been studied. The objectives of our study of Red-tailed Hawks were to: (1) determine the characteristics of selected perch sites and surrounding vegetation during the nonbreeding and breeding seasons, and (2) examine possible relationships between hunting behavior and the characteristics of perches and surrounding vegetation.

METHODS

Red-tailed Hawks were observed from October 1999–July 2000 at the Blue Grass Army Depot (BGAD), Madison Co., Kentucky. The depot encompasses 5907 ha and consists of open grassland interspersed with trees and small woodlots. We visited the BGAD 2–3 times a week during both the nonbreeding (October–March) and breeding (April–July) seasons. For each hawk observed that seemed to be hunting (scanning or looking in the direction of the ground rather than engaged in other activities such as preening or resting with eyes closed), we noted its location and, if observed landing on a perch, recorded the time spent on a perch until initiating an attack or “giving up” (changing perches or flying from the area). Once a hawk left the area, the perch substrate was identified (tree species or human-made substrate type) and marked. Perch and substrate heights were measured using a clinometer and the diameter at breast height (DBH) of the substrate measured with a DBH tape. If an attack occurred, the attack distance (measured from the perch site to the point of attack) was measured using a tape measure. Perch locations were recorded using a Global Positioning System unit (Garmin XLS, Garmin International, Olathe, KS), and these locations were used to determine distances between successive perches.

The habitat around perches was categorized as woodlot, woodrow (a strip of trees \leq 30 m wide located along abandoned fencerows and streams), edge (within 5 m of the edge of a woodlot or woodrow), mowed field (open fields with vegetation \leq 0.5 m high), or unmowed field (open fields with vegetation $>$ 0.5 m high). For statistical analysis, each habitat type was assigned a numerical value based on relative vegetation height and density (with density being our estimate of the relative density of tree trunks and branches) (mowed = 1, unmowed = 2, edge = 3, woodrow = 4, and woodlot = 5). If an attack was made, we recorded the attack distance (estimated dis-

tance from the perch to the attack site), outcome (successful or not), and, if possible, identity of the prey.

Twenty-five of 270 perches used by Red-tailed Hawks during the breeding and nonbreeding seasons, respectively, were randomly chosen and the surrounding vegetation characterized (James and Shugart 1970). In addition, 50 ‘perches,’ that to our knowledge were not used, were randomly located during the breeding ($N = 25$) and nonbreeding seasons ($N = 25$), respectively. These perches (hereafter referred to as available perches) were identified using a random number table to select map coordinates. From that location, we again used a random number table to obtain a compass bearing, then a random number of paces (0–999) taken in that direction. From that point, we selected the closest tree or human-made object that could support a Red-tailed Hawk (\geq 10 cm DBH). For both used and available perches, we identified the species of vegetation or other substrate type (e.g., utility pole) and measured the height and DBH. Three 100-m long, 3-m wide belt transects starting at the base of the perch substrate were randomly chosen (with the only stipulation being that the transects lay within 90 degrees of either side of the direction the hawk was facing at that perch or within 90 degrees on either side of a randomly-selected direction for unused sites) using a random number generator to obtain a compass bearing. At 10-m intervals along each transect, we noted the ground (bare ground, grass, forb, or shrub) and canopy cover (present or absent). The number of shrubs (<8 cm DBH) and trees (>8 cm DBH) was counted along the entire length of each transect. The density of grass and forbs was measured in 25-cm increments by passing a pole vertically through the vegetation and counting the number of vegetation contacts within an estimated 10 cm radius of the pole (Rotenberry and Wiens 1980). Vegetation height at each point was also determined.

To analyze data, the Statistical Analysis System (SAS Institute 1989) was used. Possible variation in the characteristics of perch sites and in hunting behavior (e.g., giving-up times) with season, outcome (attack or give up), and habitat was examined using repeated-measures analysis of variance. Because three analyses were conducted, we used a Bonferroni-adjusted alpha level of 0.017. Hawks were not captured and individually marked. However, for the repeated-measures analysis, those observed in particular areas were assumed to be the same individual. These areas were delineated by plotting the movements of hawks on a map of the study area. Because of occasional trespassing by neighboring individuals, the movements of migrating individuals, and possible overlap in the hunting ranges of breeding pairs, it is likely that Red-tailed Hawks other than the presumed resident individual were sometimes observed in particular areas.

All variables were tested for heterogeneity of variances and for normality. Variables that did not meet the assumptions of homoscedasticity and normality were log-transformed prior to analysis. Mean values of used and available perches were compared using multivariate analysis of variance. Wilcoxon tests were used for univariate comparisons. Stepwise discriminant analysis (backward procedure) was used to identify variables that best discriminated ($P < 0.05$) among used and available perch sites and sites used during breeding and nonbreeding

Table 1. Vegetation characteristics of perches used by Red-tailed Hawks versus available perches during the breeding season.

VARIABLE	USED ^a		AVAILABLE ^b		WILCOXON TEST <i>P</i> VALUE
	MEAN	SE ^c	MEAN	SE ^c	
Percent bare ground	8.6	1.9	7.5	1.4	0.91
Percent grass cover	86.0	3.0	81.0	2.0	0.07
Percent forb cover	2.2	0.5	5.1	0.9	0.02
Percent shrub cover	3.3	1.3	6.2	1.8	0.12
Percent canopy cover	9.0	2.0	15.0	1.0	0.01
Number of small trees	9.3	1.9	21.2	6.2	0.11
Number of large trees	2.8	0.7	7.7	1.3	0.01
Number of bushes	322.0	89.1	320.1	85.6	0.99
Vegetation contacts (<25 cm)	49.7	14.0	145.4	26.2	<0.01
Vegetation contacts (25–75 cm)	60.8	24.8	84.8	23.3	0.04
Vegetation contacts (>75 cm)	12.3	5.7	49.9	22.1	0.01
Vegetation height (cm)	20.0	2.0	34.0	4.0	0.02

^a $N = 25$, except for the variable number of bushes ($N = 21$).

^b $N = 25$.

^c Standard error.

seasons, respectively. The cross-validation technique was used to evaluate model classification efficacy (Williams et al. 1990). Cohen's *Kappa* and its *Z* value were calculated to test model performance (Titus et al. 1984). All values reported are means \pm SE.

RESULTS

Red-tailed Hawks used 270 hunting perches on 31 different types of substrates, with black locusts (*Robinia pseudoacacia*; $N = 58$), sycamores (*Platanus occidentalis*; $N = 45$), utility poles ($N = 40$), and black cherries (*Prunus serotina*; $N = 37$) used most often. Of the 50 randomly-chosen perches, 11 were black cherries (22%), 10 black locusts (20%), seven sycamores (14%), and seven white ashes (*Fraxinus americana*; 14%). Most used perches were in mowed fields ($N = 153$, 49.2%). Perches were used an average of 1.17 ± 0.03 times ($N = 269$). Mean perch height was 12.3 ± 0.3 m (range = 3.5–32.5 m; $N = 262$), while mean substrate height was 18.7 ± 0.4 m (range = 6.8–37.4 m; $N = 316$). The mean DBH of perch substrates was 44.2 ± 1.2 cm (range = 13.1–124.9 cm; $N = 279$). Mean time on perches was 8.6 ± 1.0 min (range = 0.2–151 min; $N = 284$) and Red-tailed Hawks flew a mean distance of 136.4 ± 18.9 m (range = 1–990 m; $N = 74$) to subsequent perches. Only seven attacks were observed, with Red-tailed Hawks capturing two small mammals and five unknown prey items.

Neither giving-up time ($F_{3,48} = 0.17$, $P = 0.91$)

nor perch height varied ($F_{3,50} = 0.15$, $P = 0.93$) with habitat type. In contrast, the mean time spent on perches by Red-tailed Hawks differed with outcome ($F_{1,21} = 7.87$, $P = 0.01$), with a mean perch time of 23.9 ± 12.4 min ($N = 7$) before attacks and 5.1 ± 0.5 min ($N = 214$) before giving up.

Because Red-tailed Hawks may reuse perches with particular characteristics, we compared the characteristics of perches used once to those used more than once. Analysis revealed no differences in substrate height ($F_{1,27} = 0.44$, $P = 0.51$), DBH ($F_{1,27} = 1.48$, $P = 0.23$), or habitat type ($F_{1,27} = 2.71$, $P = 0.15$).

Used Versus Available Perches. The mean height and DBH of used and available perches did not differ ($F_{1,17} < 1.14$, $P \geq 0.30$). In addition, used and available perches were located in similar habitats ($F_{1,17} = 0.13$, $P = 0.72$).

The characteristics of perches used by Red-tailed Hawks differed from available perches in both the breeding (Wilks' Lambda = 0.50, $F_{11,38} = 3.42$, $P = 0.002$) and nonbreeding (Wilks' Lambda = 0.33, $F_{11,39} = 7.29$, $P < 0.001$) seasons. For the breeding season, univariate tests revealed that seven vegetation variables differed ($P < 0.05$; Table 1), and stepwise discriminate analysis identified three characteristics that best discriminated between used and available perches during the breeding season: percent canopy cover, number of large trees, and

Table 2. Vegetation characteristics of perches used by Red-tailed Hawks versus available perches during the nonbreeding season.

VARIABLE	USED ^a		AVAILABLE ^b		WILCOXON TEST <i>P</i> VALUE
	MEAN	SE ^c	MEAN	SE ^c	
Percent bare ground	3.9	1.3	13.0	3.2	<0.01
Percent grass cover	84.0	4.0	72.0	4.0	0.01
Percent forb cover	5.5	1.6	7.0	1.9	0.56
Percent shrub cover	1.0	0.5	6.8	1.5	<0.01
Percent canopy cover	16.0	2.0	20.0	2.0	0.08
Number of small trees	4.4	2.6	51.3	16.6	<0.01
Number of large trees	4.9	1.0	10.4	2.8	0.42
Number of bushes	112.5	18.5	136.7	40.3	0.94
Vegetation contacts (<25 cm)	9.3	7.3	59.4	12.9	<0.01
Vegetation contacts (25–75 cm)	12.7	10.3	61.1	17.9	<0.01
Vegetation contacts (>75 cm)	5.6	3.8	46.7	13.1	<0.01
Vegetation height (cm)	9.0	3.0	33.0	5.0	<0.01

^a $N = 26$, except for the variable number of bushes ($N = 2$).

^b $N = 25$, except for the variable number of bushes ($N = 14$).

^c Standard error.

number of vegetation contacts below 25 cm. Analysis using these three variables correctly classified 92% of used perches and 80% of available perches (72% better than by chance alone; Cohen's *Kappa* $Z = 5.14$, $P < 0.01$).

Univariate tests revealed eight vegetation variables that differed ($P < 0.05$) during the nonbreeding season (Table 2). Stepwise discriminate analysis identified six characteristics that best discriminated between used and available perches during the nonbreeding season: percent bare ground, percent grass, percent shrub, number of vegetation contacts lower than 25 cm, number of vegetation contacts between 25 and 75 cm, and vegetation height. Analysis using these variables correctly classified 84.6% of used perches and 80% of available perches (71% better than by chance alone; Cohen's *Kappa* $Z = 6.51$, $P < 0.01$).

Seasonal Differences in Perch-site Characteristics. Red-tailed Hawk perch height did not vary with season, with a mean of 12.9 ± 0.9 m for the breeding season and 12.2 ± 0.3 m for the nonbreeding season ($F_{1,27} = 2.96$, $P = 0.097$). Also, the mean distance flown to subsequent perches during the breeding ($\bar{x} = 122.6 \pm 27.8$ m; $N = 15$) and nonbreeding ($\bar{x} = 143.1 \pm 24.9$ m; $N = 53$) seasons did not differ ($F_{1,28} = 0.01$, $P = 0.95$). Habitat surrounding perches did not vary ($F_{1,27} = 0.63$, $P = 0.43$) by season, with most perches located in mowed fields throughout the study. Differences be-

tween seasons in giving up times approached significance ($F_{1,28} = 4.66$, $P = 0.04$), with a mean giving up time of 20.8 ± 4.4 min ($N = 52$) for the breeding season and 5.8 ± 0.6 min ($N = 215$) for the nonbreeding season.

DISCUSSION

Red-tailed Hawks in our study used natural perches more than human-made perches such as utility poles, and similar results have been reported by others (Chamberlin 1974, Bohall and Collopy 1984, Bildstein 1987). Although human-made structures may provide suitable perches for raptors, the number and distribution of such structures may not be sufficient in most areas to provide access to all available hunting areas. Most perches used by Red-tailed Hawks in our study were in black locust and sycamore trees, and on utility poles. The frequent use of black locust and sycamore trees on the BGAD (38% of all perches) was likely related to abundance, with these two species comprising 34% of the 50 available trees. In addition, however, both trees have open crowns (Elias 1980), which may provide easier access to perches for Red-tailed Hawks.

The absence of utility poles in our random sample indicates that utility poles were not as abundant on the BGAD as many trees. Where available, however, Red-tailed Hawks may prefer utility poles as perches because they provide ready access and an

unobstructed view. Errington and Breckenridge (1938) also noted the use of poles and fence posts by hawks in the genus *Buteo*. Similarly, Ferruginous Hawks (*Buteo regalis*) used fence posts (Wakeley 1978, Plumpton and Andersen 1997) and other man-made substrates (Plumpton and Andersen 1997) as perches more than other substrates.

Red-tailed Hawks in our study perched at a mean height of 12.3 m. Similarly, Craighead and Craighead (1956) and Bildstein (1987) found that Red-tailed Hawks typically perched at heights of 11.0 m and 11.3 m, respectively, while Chamberlin (1974) found that perches were usually between 12.5–18.3 m high. Craighead and Craighead (1956) stated that buteos choose high, conspicuous perches to scan an area. Higher perches may provide a larger field of view (Sonerud 1992) and increase chances of detecting prey. However, prey detectability decreases as perch height increases (Andersson 1981), and higher perches also increase attack distance and the chance that potential prey will see an attacking hawk and avoid capture. For example, hunting success declined with increased attack distance in Ferruginous Hawks (Wakeley 1978). Thus, Red-tailed Hawk perch heights may represent a compromise between the need to scan as much area as possible while minimizing attack distances.

From 270 perches, Red-tailed Hawks in our study initiated only seven attacks. Chamberlin (1974) observed Red-tailed Hawks for three months in Michigan and observed just 16 attacks, with five being successful. Bildstein (1987) reported observing only 14 attacks by Red-tailed Hawks over four months in southern Ohio. Such results suggest Red-tailed Hawks initiate attacks at low rates. Preston and Beane (1993) noted that Red-tailed Hawks were opportunistic predators that focused on the largest prey readily available. This tendency, in combination with a high percentage of successful attacks (Orde and Harrell 1977), suggests that few attacks might be needed to meet a hawk's energetic needs, perhaps contributing to the low attack rates observed in our study and previous studies.

Red-tailed Hawks spent more time on perches before an attack than before giving up. Although this difference should be viewed with caution because we only observed seven attacks, investigators have also reported longer attack times than giving-up times in other raptors. For example, Bye et al. (1992) found that attack (or detection; Carlson 1985) times of Boreal Owls (*Aegolius funereus*) averaged 4.55 min and giving-up times 2.23 min. Sim-

ilarly, Sonerud (1989) noted that attack times were longer than giving-up times for Northern Hawk Owls (*Surnia ulula*). In contrast, giving-up times were longer than attack times for American Kestrels (*Falco sparverius*; Rudolph 1982) and two passerines, Eastern Bluebirds (*Sialia sialis*; Pinkowski 1977) and Spotted Flycatchers (*Muscicapa striata*; Davies 1977). The type of prey being hunted may contribute to these differences. Because mammals are more difficult to capture than insects (Temeles 1985), predators hunting mammals may wait longer before initiating an attack. For example, hawk owls wait to attack their prey after locating it to make sure it is uncovered to increase the chance of a successful attack (Sonerud 1992).

Perch-site Preference: Used Versus Available Perches. During the breeding season, hunting areas used by Red-tailed Hawks in our study had less forb cover, less dense vegetation (fewer vegetation contacts) in all three height categories, and shorter vegetation than available areas. In Arkansas, Preston (1990) found that habitat patches with greater plant cover density (e.g., tall corn and wetlands) supported greater prey biomass than patches with less cover (e.g., old fields and corn stubble). Despite such differences, Red-tailed Hawks favored old field and corn-stubble patches (Preston 1990). Other investigators have also noted that Red-tailed Hawks typically forage in areas with less cover (Craighead and Craighead 1956, Orde and Harrell 1977). With less ground cover, Red-tailed Hawks may be able to see and capture prey easier (Baker and Brooks 1981). Orde and Harrell (1977) suggested that Red-tailed Hawks preferred areas with vegetation less than 10 cm high because this increased prey vulnerability. Similarly, Preston and Beane (1996) reported that Red-tailed Hawks favored areas with sparse ground cover and, presumably, high prey vulnerability.

Hunting areas used by Red-tailed Hawks in our study were also more open than available areas, with less canopy cover and fewer large trees. Similarly, other investigators have noted that Red-tailed Hawks are typically found in more open areas than sympatric Broad-winged (*Buteo platypterus*) and Red-shouldered (*Buteo lineatus*) hawks (Titus and Mosher 1981, Bednarz and Dinsmore 1982). Because of their relatively large size (and wing-span) and apparent preference for open areas for hunting, Red-tailed Hawks may avoid areas with high densities of trees.

During the nonbreeding season, hunting areas

used by Red-tailed Hawks in our study had less bare ground, more grass cover, less shrub cover, fewer small trees, less dense vegetation, and shorter vegetation than available areas. As during the breeding season, shorter, less dense vegetation may make it easier for the hawks to locate and capture prey.

Perch-site Characteristics and Seasonal Differences. The hunting behavior of Red-tailed Hawks (perch height, distance between successive perches, and habitat used) did not vary with season, perhaps because hawks probably hunt similar prey in the same habitats throughout the year in our study area. Raptors whose food habits change with season may vary their behavior. For example, American Kestrels used lower perches when hunting insects than when hunting mammals (Bildstein 1987).

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MOVEMENTS AND SURVIVAL OF FLEDGLING COOPER'S HAWKS IN AN URBAN ENVIRONMENT

R. WILLIAM MANNAN,¹ WENDY A. ESTES, AND WILLIAM J. MATTER
School of Renewable Natural Resources, University of Arizona, Tucson, AZ 85721 U.S.A.

ABSTRACT.—Cooper's Hawks (*Accipiter cooperii*) nest in urban and suburban areas across North America, but little is known about movements, habitat use, or survival of fledglings in these settings. We followed 40 radio-tagged, fledgling Cooper's Hawks hatched in Tucson, Arizona in 1999 or 2000, for up to 6 mo to estimate survival, and describe patterns of movement and the environments they use while dispersing. The typical pattern of movement for hawks we tracked through early winter consisted of sedentary behavior in the natal area, followed by relatively long movements beginning 11–13 wk after hatching, and finally sedentary behavior again when they settled into a fall/winter home range. Distances between relocations of individual hawks were, on average, greater for females ($\bar{x} = 6.8$ km, range = 0.02–51.7 km, SD = 9.8) than males ($\bar{x} = 3.8$ km, range = 0.05–20.8 km, SD = 5.4; *t*-test, $P = 0.02$). Home range size for nine hawks during their first fall/winter averaged 771 ha (SD = 403). Distance from center of home range to natal site averaged nearly twice as far for females ($\bar{x} = 10.9$ km, range = 4.2–19.5 km, SD = 6.4) as males ($\bar{x} = 6.0$ km, range = 2.2–13.3, SD = 5.0), but the difference was not significant (*t*-test, $P = 0.23$). Survival of radio-tagged hawks was 67% through 180 d. Hawks used a variety of environments prior to settling for the winter, but were found most frequently (35% of locations) in riparian areas. We found no discernable pattern of habitat selection for land use categories inside winter home ranges. We speculate that the abundance of food may facilitate survival of post-fledging, dispersing hawks in Tucson.

KEY WORDS: *Cooper's Hawks; Accipiter cooperii; dispersal; habitat selection; home range size; urban environments; Tucson, Arizona.*

MOVIMIENTOS Y SUPERVIVENCIA DE POLLUELOS DEL GAVILÁN DE COOPER EN UN AMBIENTE URBANO

RESUMEN.—El gavilán de Cooper (*Accipiter cooperii*) anida en áreas urbanas y suburbanas a lo largo de Norteamérica, y se conoce poco acerca de sus movimientos, uso de hábitat, o sobre la supervivencia de los juveniles en estas localidades. Seguimos 40 gavilanes de Cooper juveniles equipados con radios de telemetría empollados en Tucson, Arizona en 1999 o 2000, por cerca de 6 meses para estimar su supervivencia, y describir los patrones de movimiento y los ambientes que ellos usan durante su dispersión. El patrón típico de movimiento para los gavilanes que seguimos a principios del invierno consistió de un comportamiento sedentario en el área natal, seguido por movimientos relativamente largos que comienzan en la semana 11–13 luego de romper el cascarón, y finalmente un comportamiento sedentario de nuevo cuando se establecen dentro de su rango de acción de la temporada otoño/invierno. Las distancias entre las reubicaciones individuales de los gavilanes fueron, en promedio, más grandes para las hembras ($\bar{x} = 6814$ m, rango = 16–51 673 m, SD = 9752) que para los machos ($\bar{x} = 3776$ m, rango = 46–20 759 m, SD = 5356) (test de T, $P = 0.02$.) El tamaño del rango de acción para nueve gavilanes durante su primer otoño/invierno promedió 771 ha (SD = 403.) La distancia del centro del rango de acción al sitio natal fue en promedio cerca de dos veces más lejana para las hembras ($\bar{x} = 10.9$ km, rango = 4.2–19.5 km, SD = 0.387) que para los machos ($\bar{x} = 6.0$ km, rango = 2.2–13.3, SD = 5.0), pero la diferencia no fue significativa (test de T, $P = 0.23$.) La supervivencia de los gavilanes monitoreados fue del 67% para 180 días. Los gavilanes usaron una variedad de ambientes antes de establecerse para el invierno, sin embargo se encontraron mas frecuentemente (35% de las ubicaciones) en zonas riparias. No encontramos ningún patrón discernible en la selección del hábitat para las categorías del uso del suelo dentro de los rangos de acción invernales. Especulamos que la abundancia de alimento puede facilitar la supervivencia de los gavilanes juveniles que se dispersan en Tucson.

[Traducción de César Márquez]

¹ E-mail address: mannan@ag.arizona.edu

Natal dispersal in birds is the movement of fledglings away from their nests and often involves a search by dispersing individuals for a place to reside and potentially breed. Distances traveled by dispersing birds and their survival can significantly affect the genetic structure, demography, and viability of bird populations (e.g., Pulliam and Danielson 1991, Payne and Payne 1993, Clobert et al. 2001). Natal dispersal usually is measured as the straight-line distance between natal nests and sites where birds first breed, if they survive (Howard 1960, Greenwood and Harvey 1982). But dispersal generally takes place in landscapes composed of patches that vary in size and quality relative to the needs of dispersing individuals; thus, movements between natal and breeding sites are not likely to be linear (Wiens 2001). Furthermore, selection of a place to reside by dispersing birds may be conducted in stages (e.g., search, settlement, residency; Stamps 2001), each associated with different behaviors and patterns of movement. Identifying patterns of movement in all stages of dispersal is critical to understanding why dispersing birds settle and breed where they do. Also, information about environments that facilitate movement and survival during dispersal (e.g., Miller et al. 1997) are important in the development of habitat management plans for birds, especially if plans encompass broad spatial scales (e.g., Strong and Bancroft 1994, Miller et al. 1997) and fragmented landscapes (e.g., Temple 1989).

Natal dispersal has been studied in a variety of bird species over the last decade, but information about this process remains limited compared to other aspects of population demography and other kinds of movements (Koenig et al. 2000, Walters 2000, Clobert et al. 2001). Among birds of prey, various stages of natal dispersal have been studied primarily in species that are the focus of management and conservation efforts and in environments that are relatively undeveloped or rural (e.g., Wyllie 1985, Walls and Kenward 1995, Ganey et al. 1998, Harmata et al. 1999, Restani and Mattox 2000). Cooper's Hawks (*Accipiter cooperii*) nest in highly-developed environments (i.e., urban and suburban areas) in several places across North America (see Rosenfield and Bielefeldt 1993 for review, Stewart et al. 1996, Boal and Mannan 1998, 1999), but little is known about the movements, habitat use, or survival of fledglings in these settings. Existing information suggests that Cooper's Hawks may move up to 100 km from their natal

nests in their first fall and winter (Boal 1997), but most reported movements during natal dispersal are considerably less than this distance (e.g., median = 6.4 km for males, $N = 10$; 14.4 and 79.0 km for two females; Rosenfield and Bielefeldt 1992, Rosenfield et al. 1996). Thus, the initial stages of natal dispersal by Cooper's Hawks hatched in relatively large metropolitan areas could occur within these developed environments.

Knowledge of the patterns of movement and habitat use of dispersing Cooper's Hawks in urban settings could be used to identify environments to protect or enhance as cities grow, assuming that hawk populations are a desired feature of the urban landscape. Furthermore, Boal and Mannan (1999) suggested that models of population growth of urban Cooper's Hawks are needed to understand whether some urban areas represent "source" or "sink" populations (Pulliam 1988). Estimates of survival of hawks during dispersal are critical to such modeling efforts (e.g., Lande 1988, Boyce 1992, Beissinger and Westphal 1998). We followed Cooper's Hawks hatched in an urban setting for up to 6 mo after fledging to: (1) estimate their survival from late summer through early winter; and (2) determine how far they disperse from natal sites, the kinds of environments they use while dispersing, and the characteristics of areas they use when they settle during their first winter.

STUDY AREA

We marked and tracked fledgling Cooper's Hawks in and near Tucson, Arizona (32° N, 111° W). The Tucson metropolitan area encompasses about 70 000 ha with an estimated human population of 803 600 residents. Tucson includes developments ranging from commercial districts and high-density housing to suburban areas with low-density housing. Parks, golf courses, and open space are scattered throughout residential areas. Tucson is located in the Sonoran Desert and supports remnants of lower and upper Sonoran vegetation types and riparian corridors (Brown et al. 1979), but much of the natural vegetation has been removed or replaced with nonnative plants.

METHODS

We used bal-chatri traps (Bloom 1987) to capture fledgling Cooper's Hawks at nests monitored in a long-term study (Boal and Mannan 1999, Mannan and Boal 2000). We captured fledglings when they were old enough to hunt on their own and when their rectrices were fully emerged (≥ 55 d old). We marked each captured fledgling with a Department of Interior leg band and a colored leg band with a unique alpha code, and attached a radiotransmitter (model RI-2C [5 g] in 1999 and model PD-2 [3.5 g] in 2000; Holohil Systems Ltd.,

Carp, Ontario, Canada) to a central rectrix (Samuel and Fuller 1994). Estimated life of transmitters was 6 mo (model PD-2) or 9 mo (model RI-2C). No more than two fledglings (usually a male and female) from any nest were radio-tagged, and nests from which fledglings were marked were all >5 km from the edge of the metropolitan area.

We relocated radio-tagged hawks, while they remained in their nest areas, at least once per week by "homing" (White and Garrott 1990) with Telonics TR-2 receivers and RA-14 flexible, two-element, yagi antennas (Telonics-Electronics Consultants, Mesa, AZ). After hawks left their nest areas, we attempted to relocate them by scanning for their radio signals from 40 elevated positions (e.g., hillsides, tops of buildings) once or twice per week. Elevated positions were scattered throughout most of the Tucson metropolitan area so that any radio-tagged hawk present likely would be detected. If a signal was detected from an elevated position, we estimated its general location based on signal strength, and then attempted to locate the hawk by "homing" in an automobile and on foot. In areas without elevated positions, we drove along parallel roads throughout the area and scanned for radio signals. If a hawk settled into a relatively small area where it could be found with consistency (i.e., established a home range), we attempted to relocate it up to five times per week at various times of the day by homing. We allowed at least 12 hr between relocations for any given hawk to minimize the risk of dependency among locations.

Once or twice per month, we flew in a single engine aircraft in parallel transects over the Tucson metropolitan area and scanned for radio signals. We also scanned for radio-tagged hawks while the aircraft was flown along major watercourses up to 100 km from Tucson. If a signal from a radio-tagged hawk was detected from the aircraft, we recorded the general area of the detection, and returned to the area in an automobile to search for the hawk.

Cooper's Hawks in Tucson are acclimated to the presence of humans, and single observers can approach hawks without eliciting flight (Mannan and Boal 2000). Therefore, we attempted to see the hawks at each relocation. Sometimes hawks were out of sight (e.g., in a fenced back yard), but were close enough that their radio signal could be detected with the receiver connected only to the antenna cable (i.e., with the antenna detached). In such cases, we estimated the location of the hawk to be within 30 m of the strongest signal. If a hawk was out-of-sight, in an area where we did not have permission to access, and not within 30 m of the observer, we estimated its position by triangulation. We marked all locations on an atlas of city streets.

Analyses. We plotted all locations of hawks on a digital representation of the streets and land use categories in Tucson (Shaw et al. 1996). We first measured distances between all consecutive locations of each hawk, including locations estimated from aircraft and elevated positions (i.e., in instances where we could not locate hawks by homing). We assigned all locations, except those estimated from aircraft and elevated positions, to one of five categories based on kind of development and level of human use (i.e., low-density residential areas [<7.4 resi-

dences/ha]; high-density residential areas [≥7.4 residences/ha]; open space with low human use [e.g., cemeteries, neighborhood parks, and natural open space], open space with high human use [e.g., golf courses, district and regional parks, and schools], and other [e.g., roadways, and commercial, industrial, and agricultural areas]). If hawks established home ranges during fall and winter, we used the convex polygon method to generate area-observation curves (Odum and Kuenzler 1955) for each home range to assess whether our sample of locations adequately described home range size for the period of interest. We then estimated home range sizes with the kernal method (90% isopleth; Worton 1989). We chose the 90% isopleth because it seemed to minimize fragmentation of home ranges, while excluding areas not used by hawks. We applied a smoothing technique to the boundaries of home ranges based on least squares cross validation (h). We first calculated h for the set of locations for each hawk. We then estimated size of home ranges, and applied the average h to all home ranges (Kenward 2001). We used only locations of hawks identified by sight or triangulation, and those estimated to be within 30 m of the observer, to calculate home ranges. We used program RANGES V (Kenward and Hoddler 1996) to generate area-observation curves, and Arcview Version 3.2 (Environmental Systems Research Institute 1996) with the extension "Animal Movements" (Hooge and Eichenlaub 1997) to measure distances between locations and estimate size of home ranges.

We described habitat use by dispersing hawks before they settled into winter home ranges by calculating the percent of locations (all hawks combined) in each land use category. We could not evaluate habitat selection (i.e., comparing use versus availability) during this period because our sample of locations per hawk was small and we did not have a database identifying land use on the entire area used by dispersing hawks.

We evaluated habitat selection inside winter home ranges by first overlaying outlines of the home ranges on the digital database of land use categories in Tucson (Shaw et al. 1996). We calculated the coverage of each category in each home range, compared the coverages to land use patterns shown on aerial photographs taken in 2001 to assess accuracy, and made corrections in two home ranges. We used compositional analysis (Aebischer et al. 1993) to compare the proportion of coverage of each category to the proportion of hawk locations in each category among all home ranges. We used the Kaplan-Meier (1958) method to estimate survival of radio-tagged hawks. We conducted statistical analyses in the JMP IN 3 Windows Version statistical package (Sall et al. 2001) or Resource Selection Analysis Software for Windows (Copyright 1999, Fred Leban).

RESULTS

We radio-tagged 21 hawks in 1999 (10 females and 11 males), and 19 hawks in 2000 (8 females and 11 males). We relocated the 40 hawks a total of 527 times (58.3% by sight, 22.0% with the antenna detached from the receiver in combination with triangulation, 7.4% by triangulation alone,

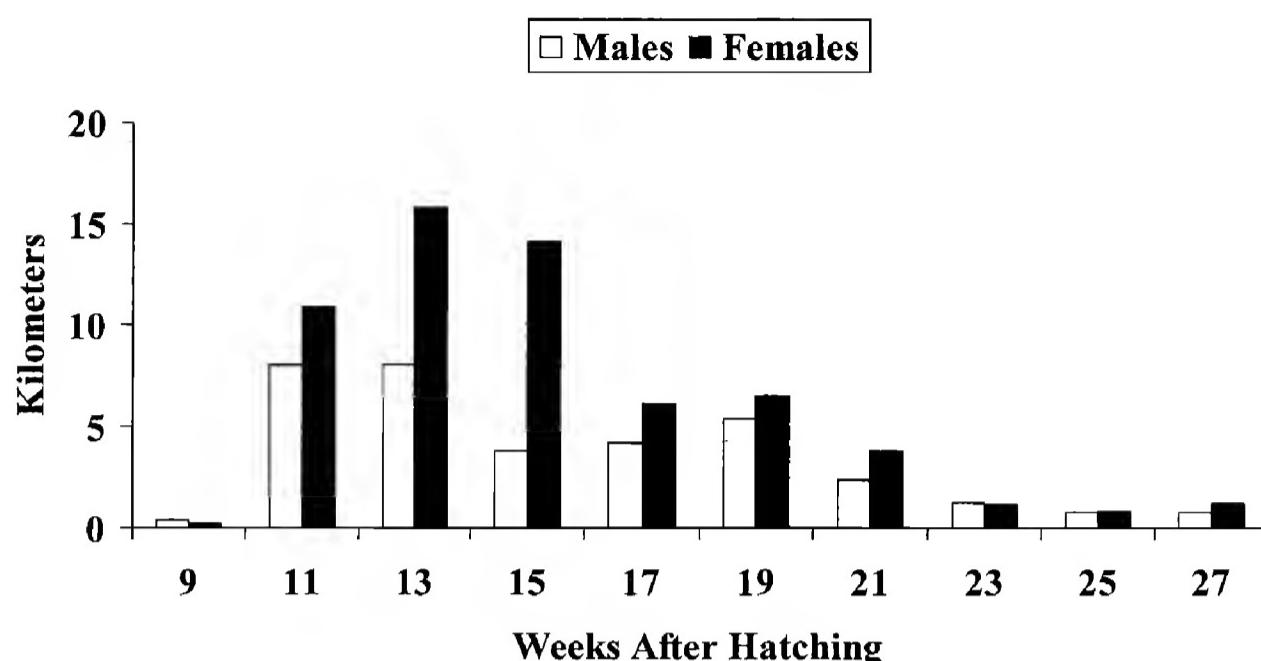


Figure 1. Mean distance between consecutive locations in 2-wk periods for radio-tagged Cooper's Hawks after fledging from nests in Tucson, Arizona, 1999–2000 ($N = 4$ –17 locations for males, and 4–13 for females, depending on period; mean number of days between locations from 11–22 wk after hatching was similar for males [$\bar{x} = 6.7$, $SD = 5.2$] and females [$\bar{x} = 7.6$, $SD = 7.4$; t -test, $P = 0.38$]).

7.4% from elevated positions, and 4.9% from aircraft). Six hawks (two females and four males) lost the tail feather on which the radio was attached, and five (three females and two males) died before meaningful information on their movements could be collected. Of the remaining 29 radio-tagged hawks, 19 (eight females and 11 males) either were located sporadically (i.e., $N \leq 9$) throughout the fall, or early in the fall but never again, and 10 (five females and five males) remained within 20 km of the Tucson metropolitan area at least into late October.

Movements. The typical pattern of movements for hawks we were able to track through early winter consisted of sedentary behavior (i.e., short inter-location distances) in the natal area, followed by relatively long movements beginning 11–13 wk after hatching, and finally by sedentary behavior again when hawks established a fall/winter home range (Fig. 1). Inter-location distances were, on average, greater for females ($\bar{x} = 6.8$ km, range = 0.02–51.7 km, $SD = 9.8$) than males ($\bar{x} = 3.8$ km, range = 0.05–20.8 km, $SD = 5.4$; t -test, $P = 0.02$; Fig. 1). One female, for example, made two movements of >59 km in a period of <20 d. Siblings did not move together after they left the natal area, and neither males nor females moved in discernable patterns prior to establishing fall/winter home ranges. We generally found hawks of both sexes in scattered locations throughout Tucson before they settled (Fig. 2).

We estimated size of home range during fall/winter for nine of 10 hawks (Table 1). Seven of the nine home ranges had become relatively stable in area by the end of our sampling period ($\leq 5.1\%$ increase in area over at least the last week of sampling), but home ranges of two females were still increasing (8.8 and 13.2%), when the hawk died or the radio failed (Table 1). We did not estimate home range size for one hawk because the sample of locations was small ($N = 11$) and was obtained during one month (December). Home range size for the nine hawks averaged 771 ha ($SD = 403$), and did not differ (t -test, $P = 0.80$) between males ($\bar{x} = 804$ ha, $SD = 456$) and females ($\bar{x} = 731$, $SD = 387$; Table 1). Distance from center of home range to natal site was nearly twice as far for females ($\bar{x} = 10.9$ km, range = 4.2–19.5 km, $SD = 6.4$) as males ($\bar{x} = 6.0$ km, range = 2.2–13.3 km, $SD = 5.0$), but the difference was not significant (t -test; $P = 0.23$). Eight of nine home ranges encompassed one or two traditional nest sites of Cooper's Hawks, but none of the dispersing hawks incorporated their natal nest sites in their fall/winter ranges.

Habitat. We found hawks in a variety of environments after they left their natal areas and before they settled into fall/winter home ranges; environments used included riparian areas (35%; a subcategory of open space), high-density residential areas (25%), low-density residential areas (22.5%), and parks and golf courses (17.5%) ($N = 40$ lo-

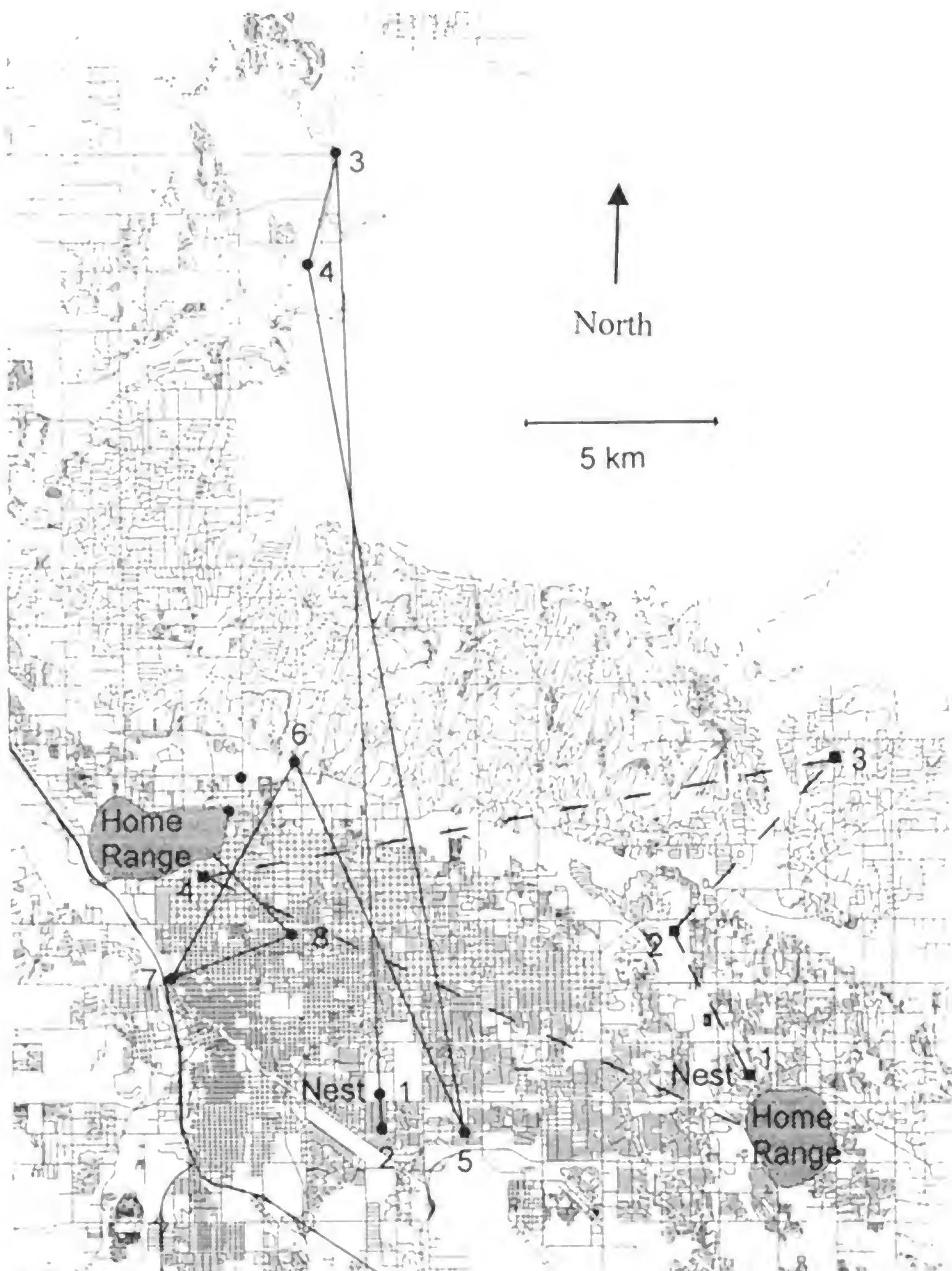


Figure 2. Sequential movements of two hawks (female = solid line; male = dashed line) between leaving their natal area and settling into a fall/winter home range in Tucson, Arizona, 1999–2000. Multiple locations in the natal area are represented by a single location.

Table 1. Size of home ranges during fall/winter, and distance from center of these home ranges to natal nests for post-fledgling Cooper's Hawks in Tucson, Arizona, 1999–2000.

HAWK ID ^a	PERIOD TRACKED IN HOME RANGE	N ^b	PERCENT INCREASE ^c	DISTANCE TO NEST ^d (km)	AREA (HA)
M327	16 Sep 99–18 Feb 00	20	4.3	2.2	492
M457	12 Sep 00–2 Dec 00	32	3.6	9.1	537
M885	11 Aug 99–8 Mar 00	73	0.0	2.2	556
M854	16 Aug 99–26 Oct 99	13	5.1	3.1	854
M313	9 Sep 00–11 Dec 00	23	3.2	13.3	1580
F215	26 Aug 00–26 Nov 00	32	8.8	4.2	409
F977	22 July 99–15 Feb 00	63	0.0	10.8	593
F276	23 Sep 00–3 Dec 00	30	13.2	9.2	628
F259	14 Aug 00–13 Nov 00	16	0.0	19.5	1294

^a M = males; F = females.

^b Number of relocations identified by sight or triangulation, and those estimated to be within 30 m of the observer.

^c Increase in area in the home range over at least the last week of sampling, representing at most the last five locations.

^d Distance from center of the winter home range to natal nest.

cations for all hawks combined, excluding those estimated from aircraft and elevated positions). Once hawks settled, their home ranges also varied in composition. Some encompassed mostly high-density residential areas, others encompassed mostly low-density residential areas, and others were dominated by cemeteries, neighborhood parks and natural open space, or golf courses and district and regional parks (Table 2). We found no discernable pattern of selection among hawks for

land use categories inside home ranges ($\chi^2 = 6.058$, df = 4, $P = 0.19$; Table 2).

Survival. Survival of radio-tagged hawks through 180 d was 67%. Two males and four females died while we were tracking them, but there was no difference in survival (Wilcoxon test, $P = 0.66$) between males (75%) and females (64%). Of the six hawks that died, two females were killed by collisions with cars, one male was electrocuted, and three died of unknown causes. Of the 10 hawks we

Table 2. Percentages of locations within five land use categories^a in home ranges of fledgling Cooper's Hawks during their first fall/winter in Tucson, Arizona, 1999–2000.

HAWK ID ^c	PERCENT OF LOCATIONS (PERCENT OF HOME RANGE) ^b				
	LOW-DENSITY RESIDENTIAL	HIGH-DENSITY RESIDENTIAL	OPEN SPACE	OPEN SPACE	OTHER
			WITH LOW HUMAN USE	WITH HIGH HUMAN USE	
M327	0.0 (6.1)	60.0 (51.4)	15.0 (21.5)	10.0 (11.7)	15.0 (9.3)
M457	78.6 (58.5)	3.6 (12.5)	7.1 (16.7)	0.0 (1.2)	10.7 (11.1)
M885	0.0 (6.7)	78.6 (52.8)	12.9 (17.3)	0.0 (1.9)	8.5 (21.3)
M854	46.1 (37.4)	7.6 (13.4)	38.5 (33.5)	0.0 (4.8)	7.8 (10.9)
M313	16.7 (7.4)	45.8 (34.3)	29.2 (37.6)	0.0 (1.2)	8.3 (19.5)
F215	36.7 (12.9)	13.3 (28.2)	3.3 (6.6)	46.7 (37.7)	0.0 (14.6)
F977	81.4 (72.1)	0.0 (3.3)	10.2 (18.4)	8.4 (5.1)	0.0 (1.1)
F276	0.0 (0.0)	50.0 (54.3)	19.2 (17.8)	26.9 (2.4)	3.9 (25.5)
F259	25.0 (24.7)	31.2 (24.9)	31.2 (39.7)	6.3 (6.4)	6.3 (4.3)

^a Low-density residential (<7.4 residences/ha); high-density residential (≥ 7.4 residences/ha); open space with low human use = cemeteries, neighborhood parks and natural open space; open space with high human use = golf courses, district and regional parks, and schools, and other = roadways, and commercial, industrial, and agricultural areas.

^b $\chi^2 = 6.058$, df = 4, $P = 0.19$; compositional analysis.

^c M = males; F = females.

were able to track through early winter, six were known to be alive 2 yr after they were radio-tagged.

DISCUSSION

The wide-ranging movements we detected among fledgling Cooper's Hawks between 11 and 22 wk after hatching are similar to those observed in related species during the early stages of natal dispersal (e.g., Eurasian Sparrowhawks [*Accipiter nisus*] in southern Scotland [Newton 1986:261]), and presumably were explorations in search of a place to settle for the winter. Environmental and social cues that triggered Cooper's Hawks to settle for the fall/winter are unknown, but rich sources of food (e.g., concentrations of birds at bird feeders), and low levels of intraspecific and interspecific competition are likely candidates. A variety of environments were used by hawks during the "exploration" period but riparian systems were used by hawks (35%) more than they generally occur on the landscape (e.g., 6% in the Tucson metropolitan area, Shaw et al. 1996), suggesting that riparian corridors may be attractive to dispersing hawks as sources of food and cover, or facilitate their movements in some manner in the urban environment.

Females disperse farther than males in many species of birds (Greenwood and Harvey 1982). Rosenfield et al. (1996) reported that the median distance moved by 10 male Cooper's Hawks during natal dispersal was 6.4 km, whereas two females moved 14.4 and 79.0 km. We found that females moved greater distances between locations than males, especially from 11–22 weeks after hatching. The wide-ranging movements of females may cause them to settle farther from their natal nests than males, but our small sample of winter home ranges and the restricted area in which we were able to follow hawks precluded definitive assessment of this relationship. The movements of hawks we report herein also may be biased in that some of the hawks we could not locate may have moved farther than those we were able to track; thus, our data may underestimate the distances moved by both sexes. It is also possible that some of the hawks we located only sporadically throughout the fall never established a home range.

Settling and establishing home ranges, even if temporary, after some period of exploration appears to be common during the early stages of natal dispersal of predatory birds (e.g., Beske 1982, Ferrer 1993, Walls and Kenward 1998). Home

ranges of Cooper's Hawks in Tucson during their first fall/winter were, on average, about 11 times larger than the home ranges of breeding males (Mannan and Boal 2000), and typically overlapped one or two traditional breeding ranges. We do not know whether the home ranges established in the first fall/winter of life persist into the following breeding season and beyond, but subsequent observations suggest that the Cooper's Hawks we radio-tagged remained in or close to them for several years. For example, four hawks (three males and one female) nested, attempted to nest, or died 2 or 3 yr after they were radio-tagged at sites that were encompassed by their first winter home ranges. Also, one male and one female hawk, radio-tagged in 2000, nested 2 yr later in sites that were 1.0 and 4.6 km, respectively, from the edges of their first winter home ranges.

Home ranges of the hawks we tracked were dominated by a variety of land use categories, and no consistent pattern of selection by hawks was evident among categories within home ranges. We speculate that Cooper's Hawks during their first fall/winter in Tucson can persist in a variety of urban environments because rich sources of food (e.g., concentrations of birds) are common and widespread (Germaine et al. 1998).

Survival of birds of prey during dispersal is low for many species (e.g., Belthoff and Ritchison 1989, Rohner and Hunter 1996, Ganey et al. 1998, but see Harmata et al. 1999) probably because fledglings are relatively inexperienced in acquiring food and avoiding predators and other agents of mortality. We found survival to be relatively high among Cooper's Hawks in Tucson for 6 mo after fledging. Abundance of food can influence survival of dispersing birds (e.g., Rohner and Hunter 1996), and we propose that an abundance of prey in Tucson may reduce mortality and offset agents of mortality common in developed environments (e.g., collisions with vehicles and windows, electrocution). Our speculation that Tucson provides ample food for Cooper's Hawks is supported by evidence that total density and biomass of birds often is higher in urban than nonurban areas (e.g., in Tucson, Emlen 1974; elsewhere, Beissinger and Osborne 1982, Blair 1996, Marzluff et al. 1998). However, our estimates of survival of fledgling Cooper's Hawks in Tucson may be biased in at least two ways. First, we could have overestimated survival because some of the hawks we could not find may have died. And second, attachment of radio-tags could

have negatively affected the hawks we studied (e.g., R. Reynolds, G. White, S. Joy, and R. Mannan unpubl. data) and led to an underestimate of survival.

Boal (1997) modeled the dynamics of the population of Cooper's Hawks in Tucson, and concluded that it was declining at about 8%/yr, primarily due to a disease (trichomoniasis) that killed about 40% of the nestlings and fledglings each year (Boal et al. 1998, Boal and Mannan 1999). The estimate of survival of juvenile Cooper's Hawks in Tucson reported herein is higher than what Boal (1997) used in his model; thus, notions about whether Tucson is a "source" or "sink" population for Cooper's Hawks could change when revised estimates of post-fledging survival are combined with updated information on adult survival, productivity, and mortality from trichomoniasis and other agents.

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NEST-SITE SELECTION AND NESTING SUCCESS OF LITTLE OWLS (*ATHENE NOCTUA*) IN MEDITERRANEAN WOODLAND AND OPEN HABITATS

RICARDO TOMÉ¹

Section of Ecology, Department of Biology, University of Turku, FIN 20014 Turku, Finland

CAROLINA BLOISE

Rua Barbosa du Bocage, 31, Lourel, 2710 Sintra, Portugal

ERKKI KORPIMÄKI

Section of Ecology, Department of Biology, University of Turku, FIN 20014 Turku, Finland

ABSTRACT.—We studied nest-site selection by Little Owls (*Athene noctua*) in two Mediterranean habitats, a holm oak (*Quercus rotundifolia*) woodland (36 nests during 1997–99) and a steppe-like area (37 nests during 1997–99), in southern Portugal, by comparing macrohabitat and microhabitat characteristics of used nests to those of randomly-selected nest sites. In the woodland area, predator presence seemed to be the main factor that influenced nest-site selection by owls. In the steppe area, a large number of alternative cavities around a nest appeared as the most important variable associated with nest-site selection. At this site, size of stones in stone piles also seemed to influence nest-site selection; owls nested in piles with larger than average stones. We also found tree girth was positively associated with nesting success in the woodland area. Larger trees held more complex cavities that may have improved the ability of adults and offspring in escaping from predators. Other variables, such as distance to human habitations and the orientation of nest-site entrance might have influenced nesting success as well. Predation risk and the internal features of nest cavities were the most likely factors affecting nest-site selection and nesting success of Little Owls in Mediterranean habitats.

KEY WORDS: *Little Owl; Athene noctua; habitat selection; Mediterranean region; predation risk; reproductive success.*

SELECCIÓN DE SITIO-NIDO Y ÉXITO EN LA ANIDACIÓN DE LOS MOCHUELOS (*ATHENE NOCTUA*) EN BOSQUES Y HABITATS ABIERTOS DEL MEDITERRÁNEO

RESUMEN.—Estudiamos la selección de sitios nido para los Mochuelos (*Athene noctua*) en dos hábitats del Mediterráneo, un bosque de roble acebo (*Quercus rotundifolia*), con 36 nidos durante 1997–99, y un área de características esteparias (37 nidos durante 1997–99) en el sur de Portugal, para comparando las características de macro y micro hábitat entre nidos y puntos seleccionados aleatoriamente. En el área boscosa, la presencia de depredadores parece ser el principal factor que influyó en la selección de sitios nido por parte de los búhos. En el área de estepa, un gran numero de cavidades alternativas alrededor del nido parece ser la variable mas importante asociada con la selección del sitio-nido. En esta área, el tamaño de las rocas en la pila de piedras parece influenciar la selección de los sitios nido: los búhos anidaron en pilas con piedras mas grandes que el promedio. En el área boscosa, encontramos una relación positiva entre el diámetro del tronco, y el éxito en la anidación. Los árboles más grandes proveen mayor complejidad que puede haber mejorado la habilidad de los adultos y su prole para escapar de los depredadores. Otras variables, tales como la distancia a las habitaciones humanas y la orientación de la entrada de los sitios nido pudieron igualmente haber influenciado el éxito en la anidación. Los riesgos de depredación y las características internas de las cavidades de los nidos probablemente fueron los factores que más afectaron la selección de sitios nido y el éxito en la anidación de los Mochuelos en los hábitats del Mediterráneo.

[Traducción de César Márquez]

¹ E-mail address: ricmocho@iol.pt

Nest-site selection is a key component of habitat selection by birds (Hildén 1965), with important consequences for survival and reproduction of individuals (Cody 1985). Nest predation is a major cause of reproductive loss in birds and is often considered as a strong selective force in the evolution of nesting and dispersal strategies (e.g., Newton 1979, Martin 1992, 1995, Hakkarainen et al. 2001). To reduce the risk of nest predation and losses due to adverse weather, birds have adopted strategies such as cavity nesting (e.g., von Haartman 1957). Consequently, cavity nesters often have higher breeding success than open-nesting species (e.g., Lack 1954, Nice 1957, Peterson and Gauthier 1985, Korpimäki 1987).

Nevertheless, high nest predation rates have also been recorded in some hole-nesting species (e.g., Flegg and Cox 1975, Dunn 1977, Eriksson 1979, Sonerud 1985b), and thus additional tactics to minimize nest predation and increase offspring production might be expected to influence nest-site selection of cavity-nesting birds. Nest-site variables, such as cavity dimensions, volume, height, and depth might be important (e.g., Stauffer and Best 1982, Van Balen et al. 1982, Peterson and Gauthier 1985, Belthoff and Ritchison 1990) and influence reproductive success (e.g., Karlsson and Nilsson 1977, Nilsson 1984, Korpimäki 1985, Rendell and Robertson 1989, Valkama and Korpimäki 1999). Microhabitat variables, such as tree species and density (Swallow et al. 1986) or the vegetation surrounding the cavity (McCallum and Gehlbach 1988, Valkama et al. 1995, Valkama and Korpimäki 1999) may also affect nest-site selection.

The Little Owl (*Athene noctua*) is a small owl mainly associated with farmland and open woodland habitats, where it breeds mostly in holes in trees, but it also uses cavities in stone piles and buildings, or even holes in the ground (Schönn et al. 1991, Génot and Van Nieuwenhuyse 2002). Over the last decades, Little Owl populations have declined severely throughout most of Europe, and the species is now listed as a "SPEC 3" species (i.e., a species whose global populations are not concentrated in Europe, but which have an unfavourable conservation status in Europe; Tucker and Heath 1994). This decrease has been caused by habitat changes due to intensification of agriculture, including elimination of nest sites, a decrease in prey abundance, and detrimental effects of pesticides on breeding success (Schönn et al. 1991, Exo 1992,

Tucker and Heath 1994, Génot and Van Nieuwenhuyse 2002).

Although several studies have described nest sites used by Little Owls, very few authors paid attention to nest-site selection strategies (Génot and Van Nieuwenhuyse 2002), particularly in steppe-like habitats. To our knowledge, only Juillard et al. (1992) and Centili (2001) reported on nest characteristics in steppe habitats, but they did not compare used nest-sites with available cavities, and thus provided no information on nest-site selection.

In western and central European farmland, where mechanization and intensification of agriculture has led to the scarcity of nest-sites, erection of nest-boxes has been adopted successfully to increase or maintain local populations of Little Owls (Kneule and Michels 1994, Bultot et al. 2001). However, in Mediterranean habitats of southern Europe, where the species is still relatively abundant, habitat features, and particularly nest sites, may be managed adequately for conservation. Therefore, our aim was to investigate features linked to nest-site selection by Little Owls in two different types of Mediterranean habitat. With this study, we collected data to develop management guidelines for the conservation of Little Owls. Furthermore, because individuals should prefer nest-site features that increase reproductive success (Alatalo et al. 1984, Leonard and Picman 1987, Milks and Picman 1994), we also examined relationships between nest-site variables and nesting success of owls.

METHODS

Study Areas. The study was conducted in two areas located approximately 22 km apart, in the Baixo Alentejo province, Southern Portugal: Cabeça da Serra (37°37'N, 8°09'W) and S. Marcos da Atabueira (37°42'N, 7°50'W). Cabeça da Serra comprised 5.6 km² of very open old holm oak (*Quercus rotundifolia*) woodland. The area is used as pasture for cattle or cereal cultivation and a small part is covered by a young plantation of stone pine (*Pinus pinea*). The density of Little Owls in this area is very high, with ca. 7 pairs/km² (R. Tomé unpubl. data). S. Marcos da Atabueira is a steppe-like area of 15.7 km² and is also used for cattle pasture and cereal cultivation. Trees are absent, with the exception of a small (<0.3 km²) plantation of blue gum (*Eucalyptus globulus*). Most of the area is managed for nature conservation. Little Owl population is less dense than in Cabeça da Serra, with ca. 2.3 pairs/km² (R. Tomé unpubl. data).

Nest-sites and Random Cavities. We searched for nests of Little Owls during the breeding seasons of 1997–99. Nest sites were mainly located by following male owls taking prey to incubating or brooding females, or young. In other cases, we detected nests by checking cavities in

places where adult birds were often observed. We measured several features of each nest site, including characteristics of the surrounding habitat. Depending on whether the nest was located in a tree or in a stone pile, the two main nesting environments for Little Owls in the study areas, we identified the tree species and measured its diameter at 1.40 m (diameter at breast height, DBH), tree height, and stone pile height, length, and width. Type of stone pile ("tower," "collapsing tower," "wall," hide for hunters, simple aggregation of stones, collapsed pile, and pile partially buried on the ground) and stability (two classes: stable, if the pile could support a person without threatening collapse; unstable, if it could not) were also classified. Mean dimensions (long and short diameters) of stones composing stone piles were determined by measuring ten stones. For nest-site entrances, we measured height (distance to the ground), long and short diameters, inclination (in degrees, corresponding 0° to a horizontal entrance and 90° to a vertical one) and orientation. For nests in trees, coverage (percent of the entrance covered by leaves or branches when viewed from 10 m, from the direction of the entrance) and site (trunk, base of branch, branch) in the tree were determined. For nest sites with more than one entrance hole, we measured the hole most often used (in all cases only one entrance hole was observed to be used). We also checked for the existence of alternative entrance holes to the same nest and for the presence of potential predator sign (e.g., feces of mustelids, foxes, rats or jewelled lizards [*Lacerta lepida*]).

We measured additional features within a 100-m radius of the nest site. We recorded the number and type of available perches and the number and type of available nesting cavities. We considered as perches any structure with a minimum height of 50 cm, because owls often hunted from perches this low. Each tree or stone pile was considered as one perch, irrespective of the number of possible individual perch sites (for instance, branches) it contained. Potential nesting cavities were defined as having a minimum depth of 50 cm and dimensions that appeared large enough for Little Owls (i.e., an opening greater than 8 cm in diameter; see also Juillard 1980, Exo 1981, Génot 1990, and Belthoff and Ritchison 1990 for the Eastern Screech Owl [*Otus asio*]). A tree or stone pile with at least one suitable cavity was considered as one available nesting site even if it had additional cavities. Other habitat features that were recorded included type of habitat and distance from the nest to the nearest road, pathway, human habitation, reservoir, and permanent stream. Distance measurements were made with the help of aerial photographs (1:15 000). Sample sizes of the variables were not equal, because it was impossible to measure all characteristics of some nests (for example, we could not be sure about the nest entrance in stone piles in some cases).

In the woodland area, 36 nests were found in 26 territories during the study period. Three different nests were used in one territory and two different nests were used in seven territories. In the steppe area, 37 nests were found in 30 territories. Two different nests were used in seven territories throughout the study. As in some other studies (e.g., Belthoff and Ritchison 1990, Sedgwick and Knopf 1990), we included all the different nests found,

because at least one of the parent owls changed in most of the territories during the study period (R. Tomé unpubl. data).

We selected 22 locations randomly for each study area and plotted these on a map with a numbered grid (e.g., Titus and Mosher 1981). Once random points were located in the field, the nearest available nesting cavity (same criteria as above) that was unused during the study period was chosen for comparison with occupied nests, and the same measurements taken.

Nesting Success. We recorded the success or failure of each nesting attempt whenever possible. This variable was 1 in cases where at least one juvenile fledged, or 0 in cases of no fledglings. Due to the depth and shape of the nest cavities, it was difficult to confirm the cause of failure in many cases (Glue and Scott 1980). Failure was ascribed to predation in cases where eggs disappeared or when we found destroyed eggs or the remains of nestlings.

Data Analysis. We compared nest-site variables between used and random cavities using parametric or nonparametric tests. Likewise, we compared variables in successful and unsuccessful nests. In three cases (one in the woodland area and two in the steppe area), nest sites were included in both categories, because they were successful and unsuccessful in different years. Continuous variables that met assumptions of homoscedasticity and normality were compared using *t*-tests. Variables that violated the assumptions were \log_e - or square-root transformed prior to analysis (Sokal and Rohlf 1981, Zar 1996), or were analyzed using Mann-Whitney *U*-tests. For categorical variables, contingency analyses were used to compare relative frequencies of used nests versus random cavities (Zar 1996). Mean cavity-entrance orientation (\bar{a} \pm angular deviation) and its dispersion (r) were calculated for both used nests and random cavities, and Rayleigh's tests (Zar 1996) were used to determine if a significant mean population existed in either sample. Differences in mean directions of entrance holes between used nests and unused cavities were examined using the nonparametric Watson's test (Zar 1996).

We used logistic regression to evaluate simultaneously the effect of different variables and their interactions on the nest-site selection and then on nesting success. These analyses treated the dependent variables as binary response variables (1 = used nest, 0 = random point and 1 = successful nest, 0 = failed nest, respectively). All variables that had a univariate *P*-value <0.25 were entered in the initial multivariate model, together with their first-order interactions (Hosmer and Lemeshow 1989). Non-significant interactions and main effects were gradually removed from the model, starting from the least significant variable. In this way, only significant main effects and interactions were included in the final model (Christensen 1990, Tremblay et al. 1997, Valkama et al. 1998). We decided not to pool data from both study areas in the analyses, because the different nature of tree and stone pile cavities resulted in basic scale and categorical differences among most variables measured. Data were analysed using SPSS statistical package (Norusis 1993).

RESULTS

Nest-site Characteristics and Nest-site Selection. Thirty-three out of the 36 nests in the woodland

Table 1. Characteristics measured in nests and random sites in the woodland area. Variables in bold with univariate *P*-values <0.25 were included in the full logistic regression model. DBH is diameter at breast height.

	NESTS MEAN ± SE	N	RANDOM SITES MEAN ± SE	N	UNIVARIATE <i>P</i> -VALUE
Tree					
DBH (m)	0.67 ± 0.16	30	0.74 ± 0.19	21	0.125
Height (m)	6.33 ± 1.98	30	6.36 ± 1.89	21	0.946
Entrance					
Height (m)	1.94 ± 0.85	34	1.79 ± 1.13	22	0.700
Long diameter (cm)	21.70 ± 12.63	33	19.14 ± 11.01	22	0.399
Short diameter (cm)	15.15 ± 9.00	33	12.20 ± 7.07	22	0.177
Inclination (°)	52.03 ± 28.31	32	56.59 ± 34.55	22	0.597
Cover (%)	8.75 ± 26.70	32	3.10 ± 13.08	21	0.487
Surroundings (100-m radius)					
No. of perches	42.42 ± 40.07	36	29.95 ± 24.25	22	0.210
No. of cavities	4.56 ± 3.17	36	3.18 ± 2.36	22	0.074
Trees/ha	4.34 ± 5.09	36	3.45 ± 3.94	22	0.163
Distances to					
Road (m)	821.39 ± 832.90	36	849.95 ± 810.89	22	0.804
Pathway (m)	114.15 ± 114.21	36	109.73 ± 91.11	22	0.972
Human^a (m)	805.25 ± 452.19	36	957.27 ± 449.85	22	0.195
Reservoir (m)	790.47 ± 483.79	36	757.55 ± 473.95	22	0.903
Stream (m)	413.50 ± 240.50	36	399.59 ± 266.60	22	0.838

^a Distance from the nest to the nearest human habitation.

area were located in trees. Two were in stone piles and one in a hole under a road. Entrance holes were located on average <2 m above the ground (Table 1). None of the continuous variables differed significantly between nests and randomly-selected unused cavities, although six variables had univariate *P*-values less than 0.25 and were entered in the initial logistic regression model (Table 1). Mean entrance orientation was $162^\circ \pm 73.1$ ($r = 0.19$) for the nests and $175^\circ \pm 72.2$ ($r = 0.21$) for the random cavities (Fig. 1a). None of the populations showed significant directionality (Rayleigh's test: $Z = 1.16$, $P > 0.20$ for nests; $Z = 0.90$, $P > 0.20$ for random sites) and there was no significant difference between the mean entrance orientation of nests and random cavities ($U^2 = 0.01$, $P > 0.5$).

Proportions of nests and random cavities did not differ significantly relative to the tree species, number of entrance holes, place of the entrance holes and habitat (Table 2). However, the proportion of nests where some predator signs were found was significantly smaller than at random sites (Table 2) and this variable was included in the initial logistic regression model.

In the steppe area, 36 nests were located in stone

piles and one in a hole in a wall. Used stone piles were on average relatively large, although low, and the nest entrance was usually situated <0.5 m above the ground (Table 3). Mean stone dimensions were significantly larger in stone piles used for nests than in unused piles (long stone diameter: $t = 3.09$, $P = 0.003$; short stone diameter: $t = 2.85$, $P = 0.006$; $N = 36$ nests, $N = 22$ unused piles; Table 3). Likewise, the number of additional suitable cavities around nests was also significantly greater than around random sites (Mann-Whitney *U*-test, $z = -2.57$, $P = 0.01$; Table 3). Nests were also significantly closer to pathways than unused piles ($t = -2.38$, $P = 0.021$; Table 3). Long stone diameter (correlated with short stone diameter: Spearman $r = 0.85$, $P < 0.001$), the number of suitable cavities, and distance to pathways were entered in the initial logistic regression model, together with small entrance diameter, which also had a univariate $P < 0.25$ (Table 3). In this area, the mean entrance orientation was $34^\circ \pm 78.1$ ($r = 0.07$) for nests and $253^\circ \pm 65.6$ ($r = 0.35$) for random cavities (Fig. 1b). None of the populations showed significant directionality (Rayleigh's test: $Z = 0.133$, $P > 0.50$ for nests; $Z = 2.50$, $P > 0.05$ for

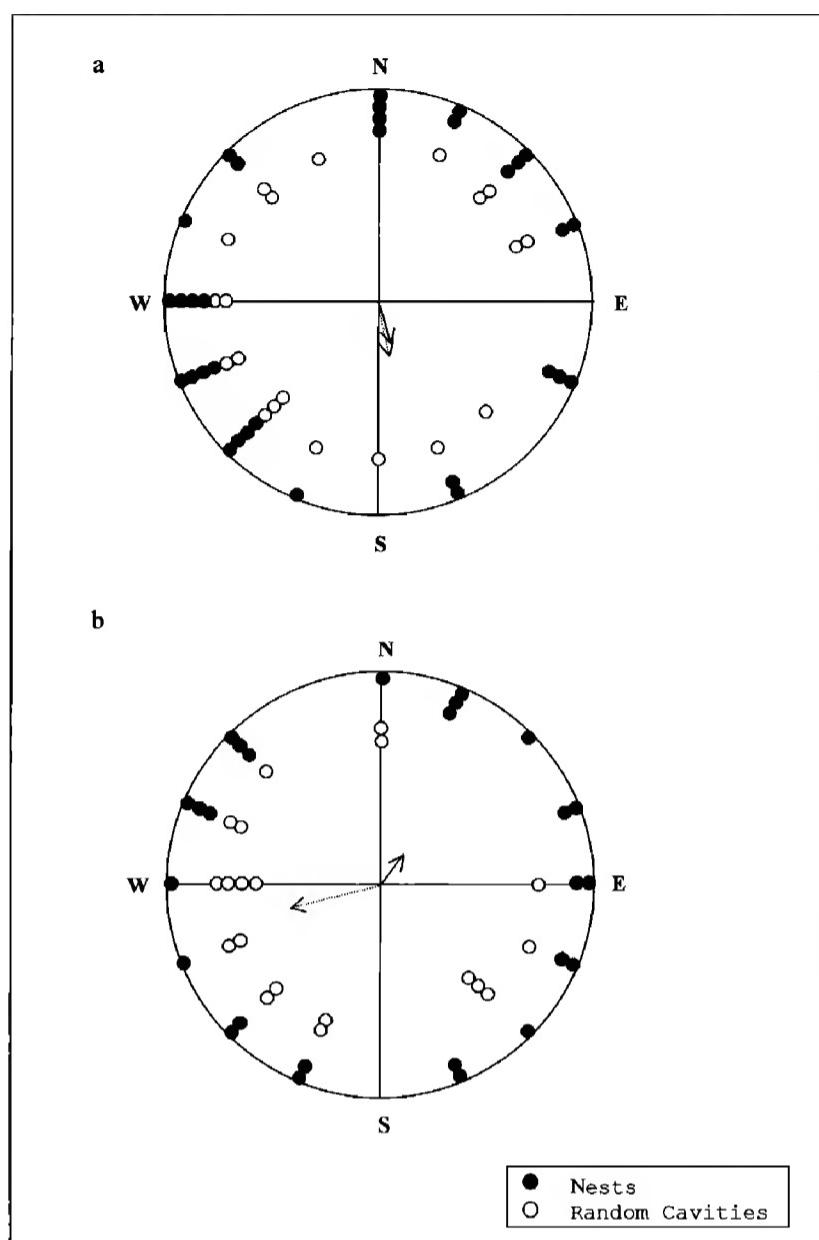


Figure 1. Cavity-entrance orientation of Little Owl nests (solid arrows) and randomly selected cavities (dashed arrows) in the (a) woodland and (b) steppe areas. Arrows represent mean direction for each distribution and their lengths correspond to the relative concentration (r ; Zar 1996) of observations.

random sites) and there was no significant difference between the mean entrance orientation of nests and random cavities ($U^2 = 0.09, P > 0.20$). The proportions of nests and random cavities did not differ significantly relative to the stone pile type, stone pile stability, habitat, and predator presence (Table 4). The proportion of nests with more than one entrance hole was significantly greater than for random sites. Four of these categorical variables showed P -values <0.25 and were therefore included in the initial logistic regression model (Table 4).

Predator presence was the only variable to enter in the final logistic regression that modelled characteristics of nests and random sites in the woodland area ($\chi^2 = 4.44, df = 1, P = 0.035$). In the

steppe area, the number of suitable nesting cavities and the long diameter of stones in piles were the two variables entering the final model (number of cavities: $\chi^2 = 4.93, df = 1, P = 0.026$; long stone diameter: $\chi^2 = 3.62, df = 1, P = 0.057$).

Nesting Success. Of all nests with known output (46 nests), 26.1% failed in the woodland area. In the steppe area, this proportion was 33.3% ($N = 45$). Almost half (48%) of the failures could be attributed to predation, although it is likely that many of the remaining nest failures were due to this factor as well (e.g., nests that were abandoned during late phase of incubation or during the nestling period).

Five continuous variables showed univariate P -values lower than 0.25 when comparing differences between successful and unsuccessful nests in the woodland area (Table 5). In successful nests, DBH was significantly larger and nests were significantly further away from human habitation (Table 5). Mean entrance orientation was $264^\circ \pm 65.8$ ($r = 0.34$) for successful nests and $25^\circ \pm 41.1$ ($r = 0.74$) for nests that failed (Fig. 2). Successful nests did not show significant directionality (Rayleigh's test, $Z = 2.79, P > 0.05$), but entrance orientation in failed nests was significantly different from a homogeneous circular distribution (Rayleigh's test, $Z = 5.52, P < 0.002$). Mean entrance orientation of the two nest types differed significantly ($U^2 = 0.46, P < 0.01$). Habitat type was the only categorical variable with univariate P -value lower than 0.25 when comparing successful and unsuccessful nests (Likelihood Ratio = 5.37, $df = 2, P = 0.068, N = 37$).

In the steppe area, none of the measured variables showed significant differences between successful and unsuccessful nests. Only stone pile height (Mann-Whitney U -test, $z = -1.78, P = 0.075, N = 36$) and type of stone pile (Fisher's Exact Test, $P = 0.089, N = 36$) showed univariate P -values <0.25 .

In the woodland area, only DBH was included in the final logistic regression model comparing the characteristics of successful and unsuccessful nests ($\chi^2 = 3.98, df = 1, P = 0.046$). Distance from nests to nearest human habitation was positively correlated with DBH (Pearson $r = 0.36, P = 0.0495$) and could be an alternative explanatory variable in the final model ($\chi^2 = 5.85, df = 1, P = 0.016$). In the steppe area, there were no significant main effects in the final model.

Table 2. Frequencies of categorical variables in nests and random sites in the woodland area. Differences were tested using χ^2 tests and Fisher's Exact Test. Variables in bold with univariate P -values <0.25 were included in the full logistic regression model. Habitat categories considered were: pasture during 3 yr (study period), young plantation during 3 yr, pasture during one part of the study, and cereal fields during another.

	NESTS (%)	RANDOM SITES (%)	TEST	P
Type of structure			Fisher's	0.75
Holm oak	29 (80.6)	17 (77.3)		
Other	7 (19.4)	5 (22.7)		
Number of entrances			Fisher's	1.00
1	28 (84.9)	19 (86.4)		
>1	5 (15.1)	3 (13.6)		
Entrance site			$\chi^2 = 2.50$	0.29
Trunk	9 (29.0)	9 (42.9)		
Base of branches	14 (45.2)	5 (23.8)		
Branches	8 (25.8)	7 (33.3)		
Habitat			$\chi^2 = 0.58$	0.75
Pasture	15 (41.7)	7 (31.8)		
Young plantation	6 (16.6)	4 (18.2)		
Pasture/cereal	15 (41.7)	11 (50.0)		
Predator			Fisher's	0.04*
Absent	25 (89.3)	7 (58.3)		
Present	3 (10.7)	5 (41.7)		

* Significant, $P < 0.05$.

DISCUSSION

Nest-site Selection. According to our results, predator presence emerged as the main factor linked to nest-site selection by Little Owls in the woodland area. Predation has also been reported as one of the major factors affecting the breeding success of this owl (Exo and Hennes 1980, Schönn 1986), and the avoidance of predators was identified as one of the most important factors when selecting a nesting site for other cavity-nesting species (e.g., Rendell and Robertson 1989).

The main predators of Little Owl nests in our study areas were mammals such as the stone marten (*Martes foina*), the common genet (*Genetta genetta*), and the garden dormouse (*Eliomys quercinus*), as well as the jewelled lizard (Knötzsch 1978, Schönn 1986, Juillard et al. 1992, Génot 2001). All these species seek shelter and roost in cavities, and thus, include a number of cavities in their home ranges. By not nesting in trees used by predators, Little Owls probably reduce the chance of being killed by a predator. An alternative hypothesis is that owls use these sites, but are able to keep most predators away from their nests. Little Owls may attack predators near nests (Glutz and Bauer 1980,

Cramp 1985); however, our observations suggest that, at least toward a human intruder, they generally limited their nest-defense actions to a few alarm calls.

The large number of suitable natural cavities in the holm oak woodland of our study area makes it unlikely that nest-site availability was limiting the breeding density of Little Owls (Exo 1983, Loske 1986, Dalbek et al. 1999). This conclusion was supported by the low use of 50 nest boxes that were available in our 4-yr study. Only one box was occupied on three occasions, by a different owl pair. Because the use of nest-boxes often indicates nest-site limitation (e.g., Lundberg and Westman 1984, Brawn and Balda 1988, Knötzsch 1988, Exo 1992 for the Little Owl), this result supports the idea that nest sites are not limiting in our study area (Brush 1983), and that owls may be able to select nest sites that are relatively safe from predators. This suggestion was supported by our results on the frequency of nesting failure and nest predation, which were relatively low when compared to data from studies on the Little Owl in other parts of Europe (Glue and Scott 1980, Exo 1983, Juillard 1984, Schönn 1986, Génot 2001).

Table 3. Characteristics measured in nests and random sites in the steppe area. Variables in bold with univariate *P* values <0.25 were included in the full logistic regression model.

	NESTS MEAN ± SE	N	RANDOM SITES MEAN ± SE	N	UNIVARIATE <i>P</i> -VALUE
Stone pile					
Long diameter (m)	8.66 ± 11.06	36	6.86 ± 5.34	22	0.569
Short diameter (m)	3.92 ± 2.00	36	4.40 ± 2.76	22	0.641
Height (m)	1.19 ± 0.74	36	1.14 ± 0.51	22	0.798
Stone					
Long diameter (cm)	31.52 ± 9.19	35	25.08 ± 6.66	21	0.003
Short diameter (cm)	19.85 ± 5.44	35	16.10 ± 3.84	21	0.006
Entrance					
Height (m)	0.45 ± 0.57	23	0.42 ± 0.29	22	0.532
Long diameter (cm)	21.32 ± 12.98	22	17.43 ± 10.92	22	0.257
Short diameter (cm)	11.20 ± 5.11	22	9.05 ± 3.60	22	0.124
Inclination (°)	71.82 ± 24.38	22	72.27 ± 28.48	22	0.542
Surroundings (100-m radius)					
No. of perches	25.84 ± 32.12	37	22.18 ± 28.81	22	0.446
No. of cavities	2.92 ± 2.75	37	1.68 ± 1.73	22	0.010
Distances to					
Road (m)	1428.43 ± 586.84	37	1333.77 ± 533.50	22	0.471
Pathway (m)	141.68 ± 123.58	37	222.14 ± 128.54	22	0.021
Human ^a (m)	1157.65 ± 404.89	37	1138.77 ± 394.99	22	0.862
Reservoir (m)	835.24 ± 363.79	37	729.05 ± 368.45	22	0.285
Stream (m)	704.81 ± 515.11	37	864.41 ± 581.23	22	0.277

^a Distance from the nest to the nearest human habitation.

In the woodland area, none of the other nest-site characteristics appeared to influence nest-site selection by Little Owls. This should be interpreted with caution, however, because it is possible that "internal" characteristics of cavities (such as length and shape of access to the nest chamber or dimensions) may influence nest-site selection. Glue and Scott (1980) and Exo (1981) mentioned that Little Owls used mainly deep chambers, reached by long and winding passages (Schönn et al. 1991). These internal cavity dimensions were not measured in our study. Moreover, the fact that we restricted the selection of random cavities to ones that seemed suitable for owls increased the realism of the test, but reduced the likelihood of finding significant differences.

In the steppe area, the number of alternative suitable cavities emerged as the main variable explaining nest-site selection. Although Little Owls often show strong nest-site fidelity (with individual variation; Glue and Scott 1980, Glutz and Bauer 1980, Ullrich 1980, Exo 1981), they may benefit

from the inclusion of alternative suitable nesting cavities in their territories. In many species of birds (Jackson 1994, Marjakangas et al. 1997, Valkama et al. 1998), including cavity-nesters (e.g., Eriksson 1979, Dow and Fredga 1983, Sonerud 1985, Hakkarainen et al. 2001; but see Korpimäki 1987, 1993), individuals avoid breeding in sites where they have failed in previous attempts due to predation, probably because predators may revisit these sites. This could select for individuals that shift nest holes between breeding attempts. The inclusion of a large number of suitable cavities in a territory may also allow Little Owls to switch to alternative sites in the case of a stone pile collapse due to erosion, and provide alternative roosting places, both for adults and fledglings (Schönn et al. 1991, Short 1979, Sedgwick and Knopf 1990). The number of potential cavities was much larger in the woodland area than in the steppe area (on average almost the double number of suitable cavities) and probably decreased the importance of

Table 4. Frequencies of categorical variables in nests and random sites in the steppe area. Differences were tested using χ^2 tests and Fisher's Exact Test. Variables in bold with univariate P -values <0.25 were included in the full logistic regression model. Habitat categories considered were: pasture during 3 yr (study period) and used for agricultural crops in at least 1 yr.

	NESTS (%)	RANDOM SITES (%)	TEST	<i>P</i>
Stone pile type			Fisher's	0.11
“Built”	5 (13.9)	7 (33.3)		
Other	31 (86.1)	14 (66.7)		
Stone pile stability			$\chi^2 = 0$	1.00
Unstable	12 (42.9)	9 (42.9)		
Stable	16 (57.1)	12 (57.1)		
Number of entrances			Fisher's	0.04*
1	16 (80.0)	22 (100.0)		
>1	4 (20.0)	0 (0.0)		
Habitat			$\chi^2 = 1.31$	0.25
Pasture	17 (46.0)	6 (27.3)		
Used for crops	20 (54.0)	16 (72.7)		
Predator			Fisher's	0.15
Absent	7 (28.0)	7 (58.3)		
Present	18 (72.0)	5 (41.7)		

* Significant, $P < 0.05$.

this variable in the final model for the woodland area.

According to our results, size of stones appeared to be an additional factor influencing nest-site selection in the steppe area, because stones in stone piles used for nesting were larger than stones in random sites. Larger stones probably create more internal cavities within piles (Juillard et al. 1992),

and also deeper cavities that owls usually prefer (Glue and Scott 1980, Exo 1981, Génot 1990). The area of nest chambers in piles of large stones should also be bigger, and for many species of cavity nesters, this is often correlated with larger clutches and higher breeding success (e.g., Karlsson and Nilsson 1977, Korpimäki 1985, Rendell and Robertson 1989, Valkama and Korpimäki

Table 5. Continuous variables that differed between successful and failed nests by univariate P -values <0.25 in the woodland area, and were included in the full logistic regression model. Differences were tested using t -tests and Mann-Whitney U -tests.

	SUCCESSFUL NESTS	<i>N</i>	FAILED NESTS	<i>N</i>	TEST	<i>P</i>
	MEAN \pm SE		MEAN \pm SE			
Structure						
Tree DBH ^a (m)	0.71 \pm 0.16	21	0.58 \pm 0.01	10	$t = 2.87$	0.008*
Surroundings (100-m radius)						
Trees/ha	3.35 \pm 2.42	26	6.48 \pm 8.31	11	$U = 101.50$	0.167
Distances						
Road (m)	982.65 \pm 843.53	26	613.73 \pm 947.85	11	$U = 89.00$	0.073
Human (m)	926.85 \pm 448.35	26	478.73 \pm 275.48	11	$t = 3.71$	0.001*
Reservoir (m)	676.19 \pm 438.01	26	1040.55 \pm 491.61	11	$U = 85.50$	0.056

^a DBH = Diameter at breast height.

* Significant, $P < 0.05$.

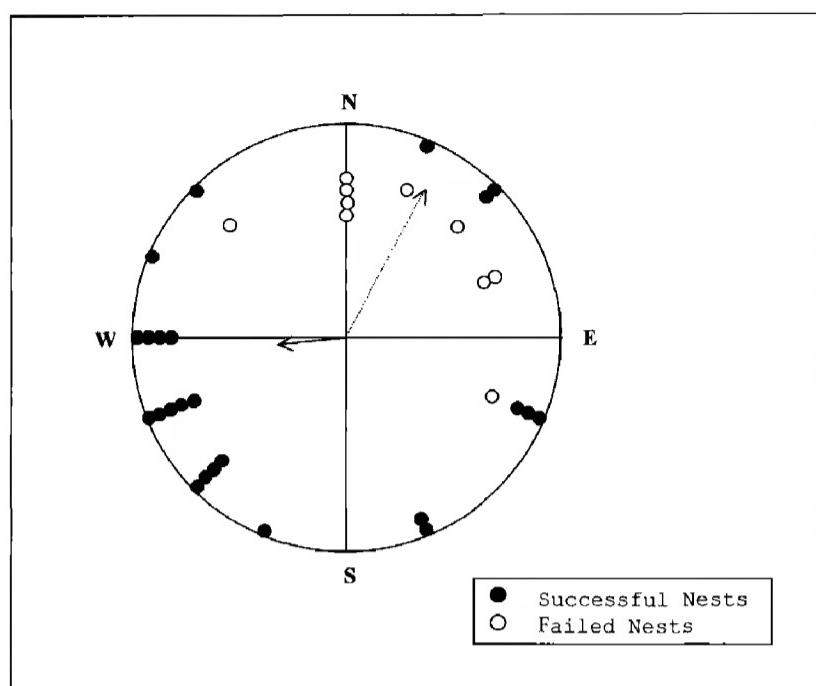


Figure 2. Cavity-entrance orientation of Little Owl nests with and without success in the woodland area. Arrows represent mean direction for each distribution and their lengths correspond to the relative concentration (r ; Zar 1996) of observations. Solid arrow—successful nests; dashed arrow—failed nests.

1999). Finally, stone piles with larger stones are usually more recent, less prone to erosion, and thus, longer lasting (Juillard et al. 1992).

Although predator frequency (predator occurrence in random points of both areas) seemed to be similar between the two study areas, in the steppe area Little Owls are apparently less able to select nest sites without predators. The relative lack of suitable cavities in this area possibly increases the probability of occupation of the same stone piles by both owls and predators. The selection of cavities with more than one entrance (or exit) seemed to have some importance in this area (Glue and Scott 1980) and might be one strategy to reduce the risk of predation.

Nesting Success. Tree diameter appeared to be linked to the nesting success of Little Owls in the woodland area, because successful nests were located in trees with a greater DBH than failed nests. By using an infrared micro-camera on 26 nests, we observed that trees with a larger diameter seemed to hold deeper cavities, with more sinuous and complex access tunnels than smaller diameter trees. By nesting in trees with a larger girth, owls possibly reduce the probability of a nest being found by predators and may increase the ability of adults and offspring to hide or to escape once predators have found the nest. Other studies have also demonstrated an inverse relationship between

depth of nest cavity and losses due to predation (Moed and Dawson 1979).

Distance to human habitations appeared to be associated positively with nesting success in the study area, but as this variable was positively associated with tree diameter, this may not represent a cause-and-effect influence. Alternatively, the possibility that predators were more numerous near human habitations could account for the higher proportion of failed nests in those areas. However, no observations indicating obvious differences in predator density are available for our study area.

Entrances in the majority of failed nests in the woodland area were towards north or northeast, which may indicate that entrance orientation could have influenced nesting success. Prevailing winds and exposure to the sun may affect energy expenditure of adults and nestlings in some cavity-nesting species, and thus influence cavity entrance orientation (e.g., Lawrence 1967, Ricklefs and Hainsworth 1968, Inouye et al. 1981, Valkama and Korpimäki 1999). For many species of owls, cavity orientation seems to be unimportant (Forsman et al. 1984, Goad and Mannan 1987, McCallum and Gehlbach 1988, Belthoff and Ritchison 1990), while other Little Owl studies show that nest entrances may (Exo 1981, Génot 1990) or may not be (Juillard 1980) protected against wind and rain.

Other variables related to nest sites might have influenced nesting success in both study areas and remained undetected. Some nests that failed very early in the breeding season may not have been detected resulting in some bias in our sample of failed nests. Although this could have hampered the identification of variables affecting nesting success, we believe that very few failed nests were missed and that it did not constitute an important bias.

Several studies have focused on the effects of large-scale and landscape variables on population dynamics of Little Owls (e.g., Van Nieuwenhuyse and Bekaert 2001, Van Nieuwenhuyse and Leysen 2001, Van Nieuwenhuyse et al. 2001, Ferrus et al. 2002). Our results show that smaller-scale features associated with nest sites may also be important and should be considered in management of Little Owl habitat. In particular, management guidelines directed towards Little Owl conservation in habitats such as the ones considered in this study could involve the preservation of large-diameter trees and stone piles made of larger stones, as well as

the maintenance of several alternative suitable cavities in the owl territories.

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STATUS AND DISTRIBUTION OF BREEDING OSPREYS IN THE CHESAPEAKE BAY: 1995–96

BRYAN D. WATTS,¹ MITCHELL A. BYRD, AND MARIAN U. WATTS
Center for Conservation Biology, College of William and Mary, Williamsburg, VA 23187 U.S.A.

ABSTRACT.—We surveyed the tidal portions of the Chesapeake Bay for nesting Ospreys (*Pandion haliaetus*) during the breeding seasons of 1995–96. The population was estimated to contain 3473 ± 75 (SE) breeding pairs. The population has more than doubled since the comprehensive survey conducted in 1973. During this recovery, there has been considerable spatial variation in the rates of population growth. Mean doubling times for well-defined subregions varied from a low of 4.3 yr to more than 40 yr. In general, growth rates have been highest in the tidal fresh and upper estuarine areas, where few pairs occurred in 1973. Based on the pattern and magnitude of the recovery, it seems that the Chesapeake Bay population experienced a greater decline during the post World War II era than was previously believed. Nesting substrate use by Chesapeake Bay Ospreys has shifted since 1973. The use of trees for nesting has declined from 31.7–7.2% in 23 yr. Channel markers accounted for 53.5% of all nest structures in the current study. Platforms established specifically for Ospreys supported 12.1% of pairs. The proliferation and diversification of artificial substrates throughout the Chesapeake Bay has been one of the most important factors contributing to recent population expansion.

KEY WORDS: *Osprey; Pandion haliaetus; Chesapeake Bay; nest substrate; population increase.*

ESTATUS Y DISTRIBUCIÓN DE ÁGUILAS PESCADORAS DURANTE SU REPRODUCCIÓN EN LA BAHÍA DE CHESAPEAKE: 1995–96

RESUMEN.—Estudiamos las porciones maréales de la bahía de Chesapeake en busca de águilas pescadoras (*Pandion haliaetus*) que estuvieran anidando durante las estaciones reproductivas de 1995–96. Se estimó que la población contenía 3473 ± 75 parejas en reproducción. La población ha aumentado mas del doble desde que el completo estudio se llevó a cabo en 1973. Durante esta recuperación, ha habido una considerable variación temporal en las tasas de crecimiento poblacional. La media de los tiempos de duplicación para sub regiones bien definidas varió desde un promedio bajo de 4.3 años a uno de mas de 40 años. En general, las tasas de crecimiento mas altas han ocurrido en las zonas de marea fresca y en las áreas altas de los estuarios, donde se presentaron pocas parejas en 1973. Con base en el patrón y magnitud de la recuperación, parece que la población de la bahía de Chesapeake experimentó un declive más grande de lo que se creía, durante la post guerra de la segunda guerra mundial. El uso del sustrato de anidación por las águilas de la bahía de Chesapeake ha cambiado desde 1973. El uso de árboles para anidar ha diminuido de 31.7% a 7.2% en 23 años. Los marcadores de canales dan cuenta del 53.5% de todas las estructuras de anidación en el presente estudio. Las plataformas establecidas específicamente para las águilas albergaron 12.1% de las parejas. La proliferación y diversificación de sustratos artificiales a lo largo de la bahía de Chesapeake ha sido uno de los factores más importantes que ha contribuido en la reciente expansión de la población.

[Traducción de César Márquez]

The Chesapeake Bay supports one of the largest Osprey (*Pandion haliaetus*) breeding populations in the world (Henny 1983). As with many similar populations, Ospreys in the Chesapeake Bay experienced dramatic declines in the post World War II era due to reproductive suppression (Truitt 1969, Kennedy 1971, 1977, Wiemeyer 1971) induced by

environmental contaminants (Via 1975, Wiemeyer et al. 1975). The Chesapeake Bay population appeared to have reached a low point by 1973 when Henny et al. (1974) estimated its size to be 1450 breeding pairs. Since that time, both reproductive performance (Reese, 1975, Henny 1977) and overall population size (Spitzer 1989, Westall 1990, Houghton and Rymon 1994) have shown remarkable recoveries.

¹ E-mail address: bdwatt@wm.edu

Henny and Ogden (1970) indicated that the magnitude of the decline experienced by the Chesapeake Bay Osprey population was considerably less than that observed further north in New England. However, estimating the size of the historical population in the Chesapeake Bay has been difficult because no bay-wide surveys were conducted prior to declines. Comparisons made between surveys conducted in the 1970s and published observations prior to 1947 for selected areas have produced varied results (Reese 1969, Stinson and Byrd 1976, Schmid 1977). These differences suggest that, even for areas within the bay, declines varied spatially.

Throughout the 1980s, evidence began to suggest that the Osprey population was approaching the carrying capacity of the Chesapeake Bay. Comparisons of selected geographic areas indicated that the number of breeding pairs had recovered to levels documented prior to the decline (Reese 1996). Sibling aggression and associated brood reduction in other locations suggested food stress (Roberts 1982, McLean and Byrd 1991, P. Spitzer unpubl. data). Available nesting substrate appeared to be saturated within selected locations and age at first reproduction had increased, likely in response to nest-site limitation (Spitzer 1989). These views were based on observations from a limited number of geographic areas. No bay-wide survey has been attempted since 1973.

Here we report the results of a comprehensive survey for Chesapeake Bay Ospreys conducted during the breeding seasons of 1995–96. We compare status, distribution, and the use of substrate types to Henny et al. (1974), and also assess spatial variation in population growth during the time period between the two comprehensive surveys.

METHODS

This study included the entire tidal portion of the Chesapeake Bay (Fig. 1). The Chesapeake Bay is the largest estuary in the United States, containing more than 19 000 km of tidal shoreline. The bay's wide salinity gradient, shallow water, and climate have made it one of the most productive aquatic ecosystems in North America. Osprey now breed throughout the estuary, from the Atlantic Ocean to the fall line. The fall line is an erosional scarp where the metamorphic rocks of the Piedmont meet the sedimentary rocks of the Coastal Plain. The geologic formations along this boundary frequently determine the landward extent of tidal influence. Over the last several decades, expansion of the human population within waterfront areas has altered the nature of the shoreline. The physical infrastructure associated with this expanding human population led to a dramatic shift in

the distribution and availability of nesting substrates for the Osprey population. Breeding Ospreys have adapted to numerous types of artificial substrates, so both distribution and abundance of breeding pairs have been influenced by the distribution of human settlement.

We located Osprey nests by piloting a small boat along the shoreline of the Chesapeake Bay and its tributaries. All tributaries were followed and surveyed to the fall line or to their navigational limits. In total, more than 800 major and minor tributaries were surveyed. Due to the size of the study area and limitations in manpower, it was not feasible to survey the entire Chesapeake Bay during a single breeding season. Portions of the bay within Virginia were surveyed during the breeding season of 1995 and those within Maryland were surveyed in 1996. We do not feel that the primary objectives (i.e., reassess population status during a narrow point in time and compare survey results to previous benchmark) of this investigation were compromised by this approach.

Because of the extensive area of coverage, it was not feasible to visit nests multiple times throughout the season. The term "occupied nest" as used here followed the definition applied in the 1973 survey (referred to as "active nests" in that survey; Henny et al. 1974). Nests were considered to be occupied if they had Ospreys on the nest or in the immediate vicinity or had evidence of use during the current breeding season. As in 1973, nearly all nests designated as occupied had attending adults or young present. One potential problem pointed out by Henny and VanVelzen (1972) and Henny et al. (1974) is that in many populations, 5–10% of individuals associated with nests are nonbreeders. Although the majority of nests surveyed had direct evidence of a breeding attempt (eggs or young present), it is possible that some nests attended by nonbreeders were included in the population estimate. Nest sites were separated into seven categories: (1) day markers, (2) light markers, (3) Osprey platforms, (4) duck blinds, (5) other man-made structures, (6) pine trees (*Pinus* spp.), and (7) hardwood trees. All duck blinds detected were recorded and mapped. The list of navigational aids from the late 1990s (United States Coast Guard 1999) was compiled for the tidal portion of the Chesapeake Bay to estimate availability of day and light markers. No attempt was made to map all platforms erected for Ospreys.

To determine growth rates for different areas throughout the Chesapeake Bay, population estimates for geographic areas defined in the early 1970s (Kennedy 1971, Henny et al. 1974, M. Byrd unpubl. data) were compared to those from the mid-1990s. Growth rates were expressed using the mean time (in years) required for the breeding population to double in size (t_{double}). Doubling time was calculated using the growth equation $N_t = N_0 e^{rt}$ where N_t is the estimated population size in the mid-1990s, N_0 is the estimated population size in 1973. Mean doubling time is estimated as $t_{\text{double}} = \ln(2)/r$.

The 1973 survey was an aerial-based survey supplemented with ground surveys over much of the study area. Henny et al. (1974) used a modified Petersen Estimator (Overton and Davis 1969) to derive a series of correction factors that were specific to both geographic area and type of nesting substrate. Correction factors were designed to account for differences in field crews between

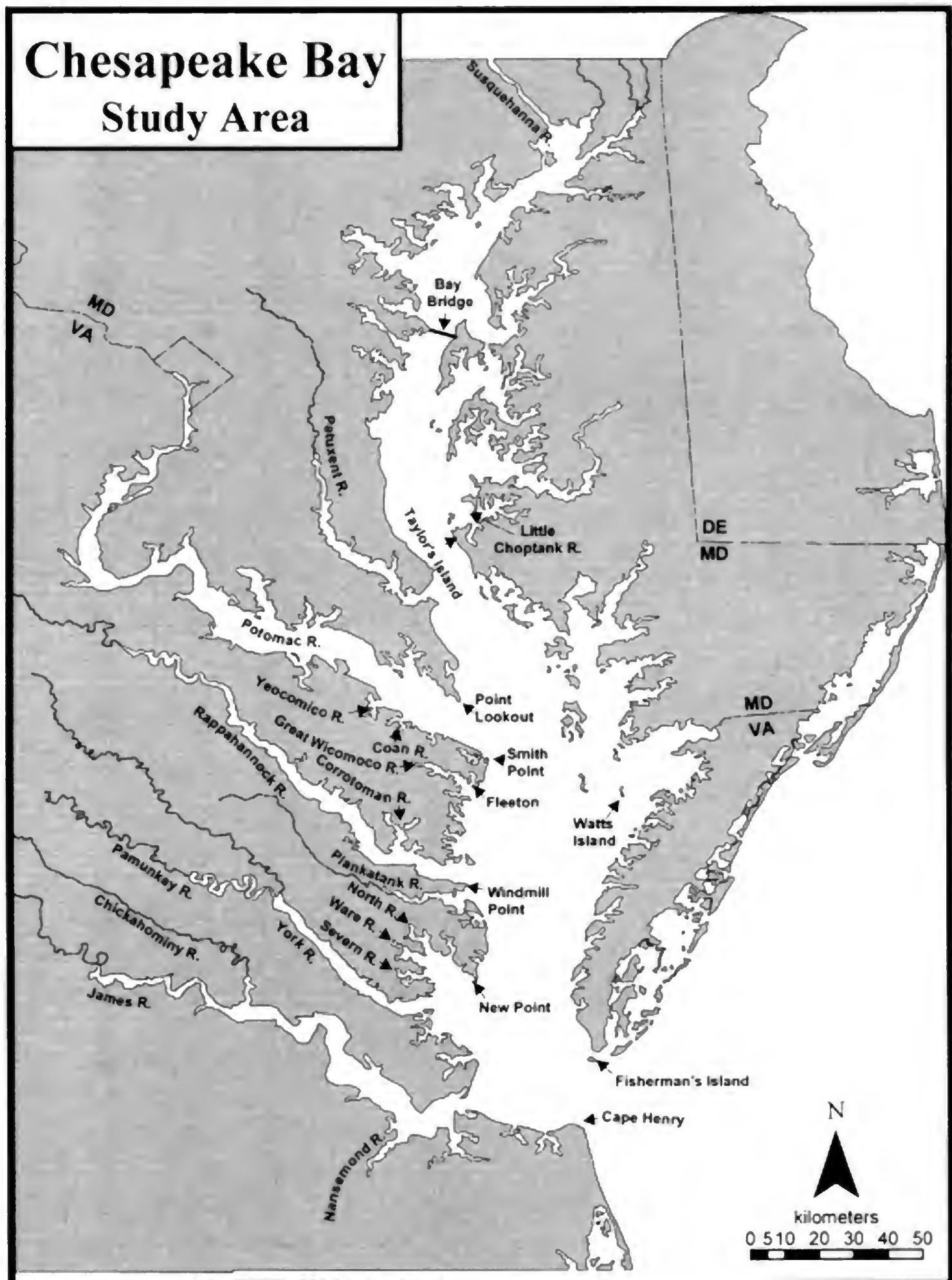


Figure 1. Map of the Chesapeake Bay study area including tributaries and landmarks used to delineate geographic areas.

Table 1. A comparison of Osprey nests detected by boat and additional nests detected from a fixed-wing aircraft inland of the shoreline (boat undercount) for ten tributaries in 1996. Mean correction factor was applied to survey results to improve the overall Chesapeake Bay population estimate.

TRIBUTARY	ADDITIONAL PAIRS DETECTED BY BOAT			CORRECTION FACTOR
	NESTS DETECTED FROM AIR			
Nansemond River	20	2	1.10	
Piankatank River	41	5	1.12	
Great Wicomico River	32	4	1.13	
Yeocomico River	29	2	1.07	
Coan River	33	5	1.15	
Corrotoman River	23	2	1.09	
Ware River	16	2	1.13	
North River	11	1	1.09	
Pamunkey River	28	4	1.14	
Severn River	18	2	1.11	
Mean (SD)			1.11 (0.024)	

geographic areas and anticipated variation in detection rates with substrate type. Nest detection rates were shown to be higher for ground surveys compared to aerial surveys across all geographic areas and substrate types. Within the areas surveyed by both techniques, 702 (88.2%) of 796 nests recorded were detected during ground surveys. Of 94 nests not detected during ground surveys, 77 (81.9%) were in trees (it was not determined how many of these were not detected by boat because they were inland of the primary shoreline).

This study used a ground-based approach and all areas were surveyed by the same field crew. We assumed that all Osprey nests over water or along the shoreline were detected (100% visibility rate) during the boat surveys. Based on detection patterns derived from the 1973 survey, this assumption may have led to an underestimate as high as 10%. Throughout the 1980s and 1990s a growing number of Osprey have colonized areas increasingly inland of the primary shoreline (B. Watts and M. Byrd pers. observ.). Most of these nests occur on cell towers, transmission towers, and other man-made structures and are not detectable from a boat. In an effort to estimate the magnitude of this inland undercount, aerial surveys were conducted along ten tributaries during the breeding season of 1996. To detect Osprey nests, a high-wing Cessna 172 aircraft was used to systematically overfly the land surface at an altitude of ca. 100 m. The aircraft was maneuvered systematically between the shoreline and a distance of approximately 1 km inland to cover the most probable breeding locations. Boat and aerial surveys were compared to determine the number of Osprey nests that were not detected during boat surveys due to their inland location (Table 1). A simple correction factor was calcu-

Table 2. A summary of Osprey pairs detected in the Chesapeake Bay by geographic area. Counts refer to breeding pairs mapped during boat surveys. Estimates were made by applying a correction factor derived from aerial surveys (see Methods and Table 1).

GEOGRAPHIC AREA	COUNT	ESTIMATE
Maryland		
Western Shore		
Susquehanna to Bay Bridge	86	95.5
Bay Bridge to Potomac River	492	546.1
Eastern Shore		
Susquehanna to Bay Bridge	162	179.8
Bay Bridge to Little Choptank River	324	359.6
Little Choptank to VA/MD Border	428	475.1
Maryland Total	1492	1656.1
Virginia		
Western Shore		
Potomac River to New Point	806	894.7
New Point to Cape Henry	680	754.8
Eastern Shore		
VA/MD Border to Fisherman's Island	151	167.6
Virginia Total	1637	1817.1
Chesapeake Bay Total	3129	3473.2

lated for each of the 10 rivers by dividing the total number of undetected (sum of boat and air) by the number of nests detected during the boat survey. The mean of these correction factors was then used bay-wide to refine population estimates.

RESULTS

We estimated the breeding population of Ospreys in the Chesapeake Bay to contain 3473 breeding pairs in the mid-1990s. Maryland and Virginia portions of the bay supported 1656 and 1817 pairs, respectively (Table 2). In Maryland, the tributaries and bays of the eastern shore supported 61.3% of the breeding pairs. In contrast, the extensive tributaries on the western shore supported 90.8% of the breeding pairs in Virginia. This difference is consistent with the distribution of open water and shoreline within these two states.

All major tidal-tributaries of the Chesapeake Bay now support large breeding populations. These include the Potomac River (797 estimated breeding pairs), James River (362), Rappahannock River (285), Choptank River (228), York River (188), Patuxent River (155), and Chester River (129). Al-

Table 3. Population comparison between 1973 and 1995–96 for geographic areas delineated by Kennedy (1971), and Henny et al. (1974). Values of r refer to intrinsic rates of increase. Values of t_{double} refer to estimated doubling time in years.

GEOGRAPHIC AREA	1971–73 ^b	1995–96	r-VALUE	t_{double}
Western Shore				
Susquehanna River to Bay Bridge	12.1	95.5	0.090	7.7
Bay Bridge to Point Lookout	38.8	390.7	0.100	6.9
Patuxent River	22	155.4	0.085	8.2
Potomac River (MD)	198.3	363.0	0.026	
Potomac River (VA)	87.5	320.8	0.059	
Smith Point Area	22	57.7	0.044	15.8
Fleeton to Windmill Point	48.7	81.0	0.023	26.4
Rappahannock River	126.7	252.0	0.031	11.7
Between Rappahannock and York Rivers	114.8	217.6	0.029	23.9
York River ^b	23.4	145.4	0.083	8.4
James River ^b	6	245.3	0.161	4.3
Chickahominy River, Eastern shore	12	115.4	0.098	7.0
Susquehanna River to Bay Bridge	69.1	179.8	0.042	16.7
Bay Bridge to Taylor's Island	242.3	359.6	0.017	40.4
Taylor's Island to Virginia Border	159.9	309.7	0.029	24.1
Virginia Shoreline and Watts Island ^b	49	125.4	0.041	17.0

^a Whole values are from total ground counts rather than corrected estimates (see Methods and Table 1).

^b Survey from Kennedy 1971.

though breeding density remains highest near the main stem of the bay, breeding pairs occur in low densities near the fall line of virtually every major tributary.

The Chesapeake Bay Osprey population has more than doubled since the comprehensive surveys conducted in 1973. Over this time period, growth rates have varied considerably among regions of the bay (Table 3). Estimated mean doubling times for well-defined geographic areas varied from a low of 4.3 yr on the James River to more than 40 yr on the eastern shore below the Bay Bridge. In general, growth rates have been highest in the upper reaches of the estuary where very few pairs occurred in 1973.

Nesting substrates used by Chesapeake Bay Ospreys shifted between 1973 and the mid-1990s. Man-made structures were used by 68.3% of the population in 1973 compared to 92.8% in the mid-1990s. Part of this shift is due to the increase in availability and use by Osprey of navigational aids. These structures represented 21.8% and 53.5% of all substrates documented in the 1973 and 1995–96 surveys, respectively. Current use is split between day (944, 30.2% of total substrates) and light markers (728, 23.3%). Osprey nesting platforms were experimental in 1973, but represented 12.1%

of all substrates used in the mid-1990s. Duck blinds have declined in relative use over the 20-yr period from 28.7–9.7%. Other man-made structures accounted for 17.6% of used substrates in the mid-1990s, and included boat houses, chimneys, docks, ships, electrical power poles, bridges, cell phone towers, and pilings. The portion of the breeding population that nested in trees declined considerably over the 20-yr period from 31.7–7.2% (5.0% pines, 2.2% hardwoods).

DISCUSSION

In little more than twenty years, the Chesapeake Bay Osprey population has more than doubled in size. The increase in numbers is obvious throughout the entire estuary. However, the growth rate over this time period has varied widely among regions within the bay. Virtually all of the areas considered to be “strongholds” for the species in the 1970s have shown relatively little growth since that time. The lack of rapid growth within these locations supports earlier suggestions that these areas were less effected by contaminants than populations elsewhere (Reese 1969, 1970). Not coincidentally, these are the same areas from which most of the ecological information concerning Chesapeake Bay Ospreys has been collected (e.g., Reese

1970, 1977, Stinson 1976, McLean 1986, Spitzer 1989). This relationship has understandably led to a limited perspective, both on the decline of the broader Chesapeake Bay population and on its recovery.

Osprey populations within the tidal fresh and brackish portions of the Chesapeake Bay have experienced the most rapid growth rates since the 1970s. In recent years, after this survey of the mid-1990s, these populations have continued to grow (B. Watts and M. Byrd pers. observ.). Comparisons for some of these areas were not included in Table 3 because they were excluded from the Henny et al. (1974) survey. These areas were not surveyed in 1973 apparently because they supported no known breeding pairs at that time. Assuming this to be true, growth rates for populations within several of these areas since that time would be the highest in the bay. The lack of any historic accounts within these areas prior to the bay-wide decline makes it difficult to determine if the lack of birds there in the early 1970s reflects the historical distribution of the species in the bay or a total population collapse. The rapid colonization of these areas throughout the 1980s and 1990s makes it difficult to believe that they were not occupied historically.

Indications that the Osprey population was reaching the capacity of the Chesapeake Bay during the 1980s, reflect conditions within the few locations for which information was available rather than bay-wide patterns. Reese (1969, 1970) documented recovery of the population below the Bay Bridge on the eastern shore to pre-DDT levels when the bay-wide population was still below 1500 pairs in the early 1970s. Ospreys within this location had the slowest growth rates compared to all other identified areas (Table 3). In Mobjack Bay, where an increase in sibling aggression and brood reduction was documented between the 1970s (Stinson 1976) and the 1980s (McLean 1986), the population has remained relatively stable since the mid-1980s (M. Byrd unpubl. data). No information is currently available on the occurrence of food stress throughout different geographic areas or its importance to the bay-wide population. Saturation of available nesting substrate has been documented along the Choptank River (Spitzer 1989). Substrate limitation is a widespread and natural condition throughout the bay especially within areas with extensive wetlands devoid of trees. The dramatic response of breeding Ospreys to nest platforms established on Smith Island (Rhodes 1972)

reflects this limitation. However, from a bay-wide perspective, the continued expansion of the human population throughout the Chesapeake Bay estuary has provided for a consistent increase and diversification of nesting structures for breeding Ospreys.

Aside from the banning of key chemical compounds, the increase in nesting substrates has likely been the most important factor fueling the recovery of the Chesapeake Bay Osprey population. The change in substrate use between the early 1970s and the mid-1990s continues the ongoing shift of Chesapeake Bay Ospreys to artificial structures that has been apparent throughout the latter half of the twentieth century. All accounts prior to 1950 describe nearly all Osprey nests observed as in either live or dead trees (Jones 1936, Tyrrell 1936, Reese 1969). In 1973, more than 65% of Ospreys were nesting on man-made structures (Henny et al. 1974). By the 1990s this portion of the population had increased to more than 90%. In just 50 yr time, the population has progressed through an almost complete shift from trees to artificial structures.

Numerous classes of structures have contributed to the shift in substrate use. Osprey nesting platforms were not in use in the Chesapeake Bay until the 1960s and 1970s (Reese 1970, Rhodes 1972). The widespread placement of platforms by the general public during the 1980s and 1990s has greatly improved substrate availability in many areas. No attempt was made during boat surveys to determine the availability of platforms. However, 380 Osprey pairs were nesting on such platforms. Duck blinds have been common throughout the Chesapeake Bay at least since the 1920s but have fluctuated dramatically in numbers through the decades (Stotts 1958, Henny et al. 1974). Approximately 3000 duck blinds were mapped during shoreline surveys including just over 300 that were more than 25 m offshore. Ospreys rarely utilize duck blinds that are not isolated from the shoreline. A total of 303 duck blinds supported nesting pairs, during the current survey suggesting that nearly all isolated duck blinds were used.

Aides to navigation or "channel markers" have become the most common substrates used for nesting by Ospreys throughout the Chesapeake Bay. In 1973, Henny et al. (1974) report 316 nests on channel markers. These pairs represented 21.8% of the population. There were 1875 navigational structures maintained in the bay in 1973, suggest-

ing an occupation rate of just below 17%. In the mid-1990s we recorded 1672 nests on channel markers representing 53.4% of nests counted during boat surveys. These included 944 on day markers and 728 on light markers. In the late 1990s, the U.S. Coast Guard listed 1680 day markers and 1249 light markers maintained throughout the Chesapeake Bay (United States Coast Guard 1999). This suggests an occupation rate of 56.2% and 58.3% for day and light markers, respectively, and a combined occupation rate of 57.1%. Clearly the increase in navigational structures from 1875–1929 over the 20-yr period has elevated their relative importance to Ospreys in the bay. It is also likely that the attitude of the Coast Guard toward nesting Ospreys has increased the occupation rates. Throughout the 1960s and early 1970s it was standard operating procedure for the Coast Guard to remove Osprey nests from navigational aides during any period of the nesting cycle or to alter structures to prevent nesting. A shift to a more Osprey-friendly policy during the late 1970s has likely had a positive impact on the bay-wide population.

In terms of factors relevant to the Osprey breeding population, the Chesapeake Bay is a different system than it was during the early 1970s. Likewise, the bay in the 1970s was a different place than it was during historical times. Fish populations have changed, the shoreline has undergone rapid alteration, and structures suitable for nesting have increased. Based on available information, it has not been possible to determine the size of the historical, bay-wide Osprey population. Given ongoing changes in the bay system that are functionally relevant to the Osprey population, it is also not clear that historical status and distribution information would be useful in predicting current and future population patterns. However, based on the variation in recovery rates throughout the bay, it does appear that the population experienced a decline of a greater magnitude than was previously believed. Additional benchmark surveys will be required to project when and under what circumstances the bay-wide population may begin to approach some upper limit.

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PARTIAL MIGRATION AND WINTERING USE OF FLORIDA BY OSPREYS

MARK S. MARTELL¹

The Raptor Center at the University of Minnesota, 1920 Fitch Avenue, St. Paul, MN 55108 U.S.A.

MICHAEL A. McMILLIAN

Archbold Biological Station, 300 Buck Island Ranch Road, Lake Placid, FL 33852 U.S.A.

MATHEW J. SOLENSKY

The Raptor Center at the University of Minnesota, 1920 Fitch Avenue, St. Paul, MN 55108 U.S.A.

BRIAN K. MEALEY²

Falcon Bachelor Bird of Prey Center, 3280 S. Miami Avenue, Miami, FL 33129 U.S.A.

ABSTRACT.—We used satellite-monitored radiotelemetry to track 14 Ospreys (*Pandion haliaetus*) breeding on three study areas in southern Florida and four Ospreys breeding along the coast of Maine. Seven birds (50%) migrated from Florida to South America and one was tracked along its migration route and at its nonbreeding season destination in successive years. Four (29%) moved from their breeding areas, but stayed in Florida. Two birds (14%) remained in their breeding areas year round. One bird died (7%) before meaningful data could be collected. Ospreys migrating to South America left their nesting grounds 16 July–27 August and arrived on South American nonbreeding areas 31 July–11 September. The seven Ospreys spent between 142–180 d in South America and initiated northward migration 10–31 January. On average they traveled 4105 km, taking 25 d ($N = 7$), with a mean speed of 178 km/d ($N = 5$). Ospreys that remained in Florida departed nesting areas 13 May–20 July. Departure from Florida nonbreeding areas was between 28 October and 9 December ($N = 4$). Mean time spent on nonbreeding areas in Florida was 154 d ($N = 3$). From Maine, two birds went to Florida (St. Lucie and Indian River counties) and two went to the Caribbean (Haiti and Jamaica). These data show that some southern Florida breeding Ospreys migrate to South America, and some northern breeding Ospreys winter in Florida.

KEY WORDS: *Osprey; Pandion haliaetus; Florida; migration; satellite telemetry; wintering area.*

MIGRACIÓN PARCIAL Y USO INVERNAL DE LA FLORIDA POR ÁGUILAS PESCADORAS

RESUMEN.—Usamos el monitoreo vía radiotelemetria satélite para seguir 14 águilas pescadoras (*Pandion haliaetus*) que anidaron en tres áreas de estudio en el sur de Florida y 4 águilas pescadoras que anidaron a lo largo de la costa de Maine. Siete aves (50%) emigraron de Florida a Sudamérica y una fue seguida a lo largo de su ruta de migración y a su lugar de destino durante la temporada no reproductora en años sucesivos. Cuatro águilas (29%) se movieron de sus áreas de reproducción, pero permanecieron en la Florida. Dos aves (14%) permanecieron en sus áreas reproductivas todo el año. Un ave murió (7%) antes de que algún dato significativo pudiera ser colectado. Las águilas pescadoras que emigraron a Sudamérica dejaron sus territorios de anidación entre 16 julio–27 de agosto y arribaron a Sudamérica a sus áreas de invernación del 31 de julio al 11 septiembre. Las siete águilas pasaron entre 142–180 días en Sudamérica e iniciaron su migración hacia el norte entre el 10 y el 31 de enero. En promedio viajaron 4105 km, tomando 25 días ($N = 7$), con una velocidad media de 178 km/día ($N = 5$). Las águilas pescadoras que permanecieron en la Florida se marcharon de sus áreas de anidación entre el 13 mayo–20 julio. La partida de las águilas de sus áreas no reproductivas en la Florida fue del 28 de

¹ Present address: Audubon Minnesota, 2357 Ventura Dr., Suite 106, St. Paul, MN 55125 U.S.A.; e-mail address: mmartell@audubon.org

² Present address: Institute of Wildlife Sciences, 10910 Cameron Ct., Suite 103, Davie, FL 33324 U.S.A.

octubre al 9 de diciembre ($N = 4$). El tiempo promedio que pasaron en las áreas no reproductivas en la Florida fue 154 días ($N = 3$). Desde Maine, dos aves fueron a la Florida (St. Lucie y los condados de Indian River) y dos al Caribe (Haití y Jamaica). Estos datos muestran que las águilas pescadoras que anidan al sur de la Florida migran a Sudamérica, y que algunas que anidan en el norte pasan su invierno en la Florida.

[Traducción de César Márquez]

Ospreys (*Pandion haliaetus*) nest from southern Florida north into Canada along the Atlantic and Gulf Coasts of North America (Poole 1989, Houghton and Rymon 1997). While most North American Ospreys winter in Latin America (Henny and Van Velzen 1972, Poole 1989), biologists have commonly believed that south Florida Ospreys do not migrate, and remain near their breeding grounds year-round (Poole 1989). Also, Florida has not been thought of as a wintering area for more northerly-breeding individuals.

Recent advances in satellite-monitored telemetry have allowed study of migratory patterns of birds large enough to carry the radios. Studies have revealed patterns of movement, timing, and wintering areas of a number of avian species, including Ospreys in Europe (Kjellen et al. 1997, Hake et al. 2001) and North America (Martell et al. 2001, Rodriguez et al. 2001).

We report here on: (1) the migratory movements of Ospreys breeding in Florida, (2) local movements of Florida breeding Ospreys, and (3)

the winter use of southern Florida by Ospreys that breed in the northern United States.

METHODS

Study Areas. We studied Ospreys in three study areas in southern Florida (27.5° – 25° N latitude): Lake Istokpoga in Highlands County, Buoy Key Island in Everglades National Park, and Sanibel Island in Lee County (Fig. 1). Lake Istokpoga has one of the highest concentrations of breeding Ospreys in the world with a population of nearly 250 pairs nesting around an 11 207 ha lake. Annual population monitoring and banding of nestlings has been ongoing since 1991. The population in Florida Bay, Everglades National Park is less dense and consists of ca. 80 nesting pairs (O. Bass pers. comm.). Studies of this population have been conducted since the 1960s (Ogden 1977). Sanibel Island Ospreys have been monitored since 1978 with over 350 chicks banded and a current population of ca. 100 pairs (M. Westall pers. comm.). In Maine we tagged birds with satellite transmitters on Sutton Island, located at ca. $44^{\circ}16'N$, $68^{\circ}15'W$, near Acadia National Park on the Atlantic coast. The most recent estimates place Maine's Osprey population between 13 000–18 000 nesting pairs with the densest concentrations along the coast (Houghton and Rymon 1997).

Satellite Telemetry. From 1999–2001, we attached 30—

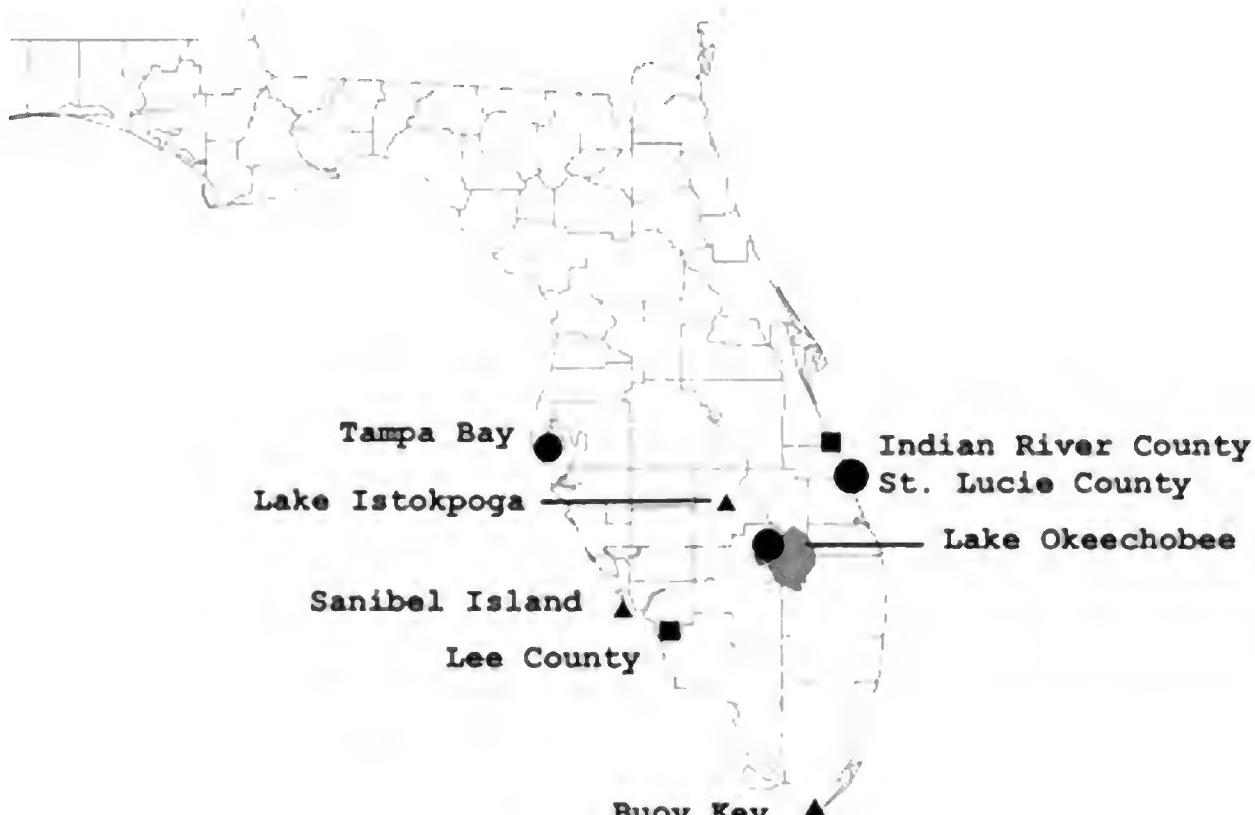


Figure 1. Study areas (triangles), non-breeding season areas of southern Florida Ospreys (circles), and wintering areas of northern breeding Ospreys (squares).

Table 1. Movement patterns of Florida breeding Ospreys, by year of trapping, gender, and breeding area.

	YEAR OF TAGGING			GENDER		BREEDING AREA		
	1999	2000	2001	F	M	ISTOK-POGA	SANIBEL	FLA. BAY
Migrated to So. America	4	1	2	6	1	7	0	0
Moved within Florida	0	4	0	4	0	2	2	0
Stayed on breeding area	0	2	0	1	1	0	1	1
No Data	0	1	0	1	0	0	0	1
Total	4	8	2	12	2	9	3	2

35 g battery or solar-powered satellite linked radiotelemetry units (PTTs; Microwave Telemetry, Columbia, MD) to 14 adult Ospreys in Florida (12 females and two males, no members of the same breeding pair), and two breeding pairs of adult Ospreys in Maine. PTTs were attached with Teflon ribbon (Bally Mills, Bally, PA) using a backpack method (Martell et al. 2001).

Birds were trapped using a noose carpet on the nest. All trapped and tagged birds were banded with standard U.S. Geological Survey aluminum leg bands and an alpha-numeric coded color leg band. From 1995–2001, M. McMillian fitted 600 nestling Ospreys on Lake Istokpoga with standard USGS bands, and a unique combination of color bands. Since 1993, B. Mealey banded 153 Osprey chicks in Florida Bay. Long-term studies were not conducted in Maine.

Satellite data were mapped and plotted using ArcView (GIS; Geographic Information System ESRI, Redlands, CA). We calculated distances by connecting “best of day” points along the route using an orthographic projection (Martell et al. 2001). Band recovery distances were measured as straight lines between banding and recovery points using ArcView GIS orthographic projection.

RESULTS

Florida Breeding Ospreys. One (7%) radio from Buoy Key stopped working after 14 wk, precluding collection of meaningful data; we suspect this bird died. Seven birds (50%), six females and one male, all from Lake Istokpoga, migrated out of Florida to South America (Table 1, Fig. 2). One bird with a radio that transmitted into a second season reused its migration route and nonbreeding season destination.

Four (29%) birds moved off their breeding area, but stayed in Florida. From Lake Istokpoga, one bird moved east to St. Lucie County on the Atlantic coast, while a second moved south to Lake Okeechobee (Fig. 1), both in two successive years. From Sanibel Island one bird moved north to the Tampa Bay area (in 2 successive years), while a second moved east across the state to St. Lucie County. Two birds (14%) remained on their breeding areas

(on Sanibel and Florida bays, respectively) year round.

Timing and Distance. Florida Ospreys migrating to South America left their nesting grounds later, and traveled longer and farther than Ospreys that migrated within Florida (Table 2). Two South American migrants tracked in successive years departed within 6–7 d of the same date in both years.

We have full return migration data for only two birds. One traveled from Venezuela in 2001 and 2002 in 7 d (averaging 389 km/d) and 10 d (272 km/d), respectively. Compared to post-breeding movements to South America, return trips during spring were 10 d (2001) and 5 d (2002) shorter. The return route was shorter (by a mean of 310 km; see routes below) and flown more quickly (a difference of 109 km/d in 2001 and 72 km/d in 2002). The second bird also traveled from Venezuela in 2001, but took 1 d more and averaged 28 km/d less on the return flight than going south.

Migratory Routes and Non-breeding Areas. Migrants leaving for South America flew south from Lake Istokpoga, along the Florida Keys, then across the ca. 200 km expanse of the Florida Straits to the Bahia de Santa Clara area of Cuba, ca. 200 km east of Havana. The birds continued southeast across Cuba, to Hispaniola, then across the Caribbean. Landfall in South America was between Lake Maracaibo, Venezuela and the mouth of the Magdalena River in Colombia. From there the birds continued to their respective wintering grounds (Fig. 2). Spring and fall routes were similar with one notable exception. One bird used Hispaniola on the southward journey in both 2000 and 2001, but took a more westerly route on the northward journey, avoiding Haiti and staying over water from Venezuela to Cuba.

Florida nesting Ospreys wintered in South Amer-

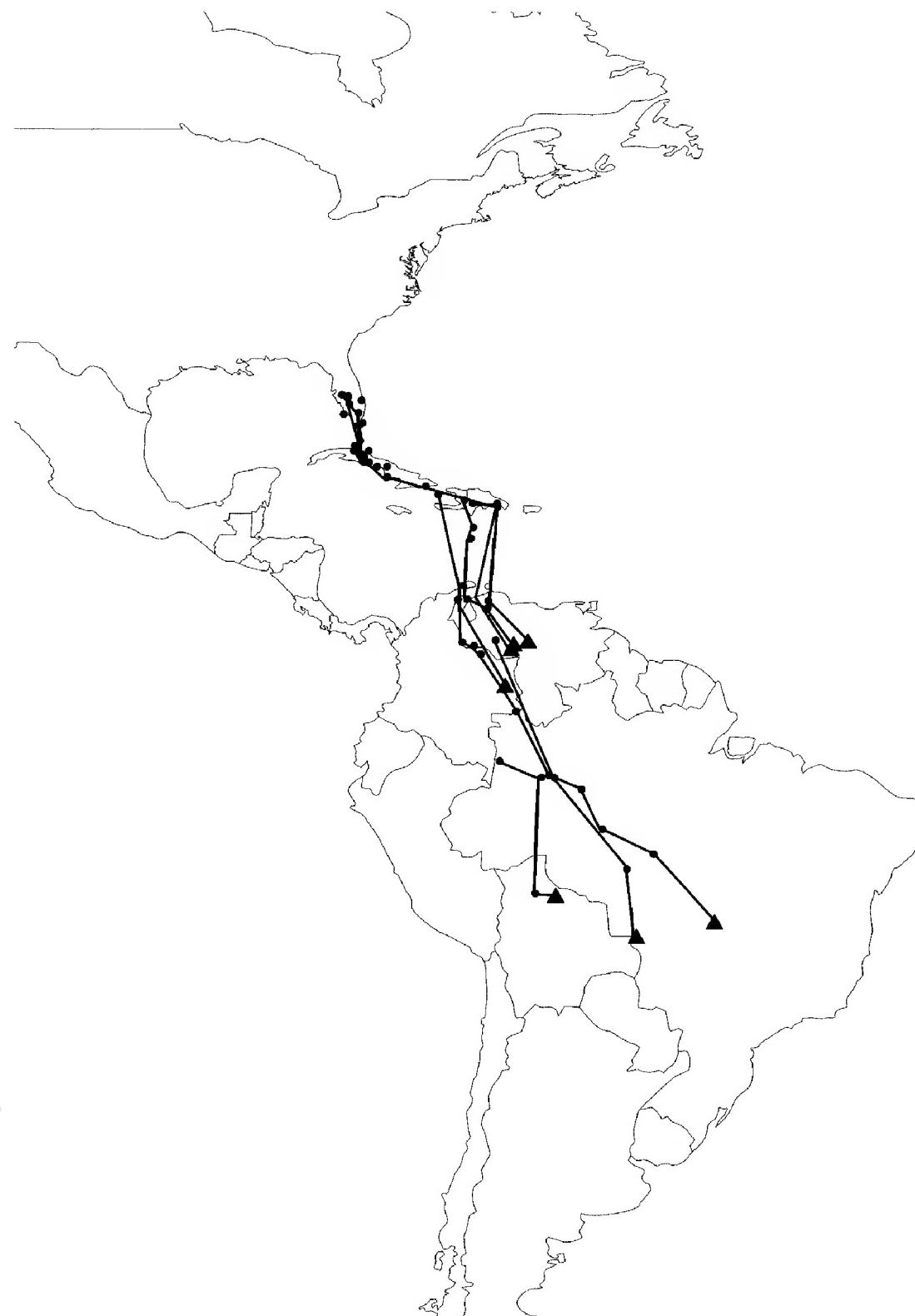


Figure 2. Migratory routes of Florida breeding Ospreys (circles = locations during migration, triangles = nonbreeding areas).

ica from 3.4°N to 16.70°S and 51.6°W to 68.5°W in Venezuela (3 birds), Brazil (2 birds), Colombia (1 bird), and Bolivia (1 bird) (Fig. 2). All Ospreys tracked more than 1 yr ($N = 4$) returned to the same nonbreeding area in successive years.

Ospreys that stayed in Florida appeared to take the most direct route to their wintering area. Birds from Sanibel went to Tampa on the western side of the state and also St. Lucie County on the eastern side of the state. One bird from Lake Istokpoga went to St. Lucie County (Fig. 1).

Band Returns. There have been 20 recoveries of birds banded as nestlings on Lake Istokpoga. Three juvenile Ospreys and one 2-yr-old were recovered in South America (20%); two juveniles and one 3-yr-old bird were recovered in the Florida Keys south of the study area (15%); three juveniles, two 2-yr-old, and two 3-yr-old birds were recovered on the Gulf or Atlantic coasts of Florida and Georgia (35%); and one juvenile and five 2–5-yr-olds were recovered from central Florida near Lake Istokpoga (30%). Four Ospreys banded as nestlings

Table 2. Timing, distance, and daily progress of migration by Florida breeding Ospreys.

	OSPREYS MIGRATING TO SOUTH AMERICA	OSPREYS MIGRATING WITHIN FLORIDA
Departure from breeding ground		
<i>N</i>	9 ^a	5 ^b
Median	27 July	25 May
Range	16 July–27 August	13 May–20 July
Distance traveled		
<i>N</i>	7	3
Mean	4105	145
Range	2964–6133	96–205
Days in travel		
<i>N</i>	7	
Mean	25	All arrivals occurred on same
Range	14–43	day as departure
Mean daily speed (km/day)		
<i>N</i>	5	
Mean	178	
Range	151–206	
Arrival at nonbreeding site		
<i>N</i>	8 ^c	
Median	26 August	
Range	31 July–11 September	
Days at nonbreeding site		
<i>N</i>	4	3
Mean	154	154
Range	142–180	134–170
Departure from nonbreeding site		
<i>N</i>	4	4
Median	27 January	9 November
Range	10–31 January	28 October–9 December

^a Includes two birds leaving 6 and 7 d apart respectively in successive years.

^b Includes two birds leaving 3 and 30 d apart, respectively, in successive years.

^c Includes one bird that arrived 8 d apart in successive years.

in Florida Bay were recovered on the east coast of Florida (two as juveniles, one 1-yr-old, and one 4-yr-old).

Northern Ospreys Wintering in Florida. Two of four Ospreys tagged in Maine, a male and female not from the same nesting pair, and a male from Shelter Island, NY (reported in Martell et al. 2001) wintered in Florida. Both males wintered in the St. Lucie/Indian River County area on the Atlantic Coast, while the female wintered in Lee County, near Sanibel Island (Fig. 1). The male from Maine used its Florida wintering area in two successive years, spending 183 and 165 d from October–

March. The second male spent 163 d from 8 October–19 March. The female from Maine spent 188 d from 30 September–6 April.

DISCUSSION

Our telemetry and banding data show conclusively that the Osprey population breeding in southern Florida is partially migratory with some individuals migrating long distances, others migrating shorter distances within the state, and a third group that does not leave their breeding grounds. To our knowledge this is the first documentation that some south Florida Ospreys are mi-

gratory (see Poole 1989). Also, our documentation of northern-breeding birds wintering in Florida shows that Ospreys present in southern Florida during the nonbreeding season cannot be presumed to be local, year-round residents. Ospreys use southern Florida for both breeding and wintering and during spring and fall as a migratory route to and from Latin America (Martell et al. 2001).

Our data on Florida birds was heavily biased toward females (12 females versus two males) and breeders from Lake Istokpoga (9/14 tagged birds). Satellite telemetry studies done on Ospreys from the northern United States showed gender-specific differences in timing and wintering locations (Martell et al. 2001). It is possible that south Florida Ospreys would also show gender-based differences with a larger sample size of male birds.

Fifty percent of the satellite-tracked birds we studied, and 20% of the band recoveries from Lake Istokpoga, showed complete migrations to South America. These Florida birds are true migrants, showing both similarities and differences in their migration patterns when compared to other North American Ospreys. Birds in this study used the same routes through the Caribbean and South America as Ospreys from northern states (Martell et al. 2001), and they also showed the same multi-year fidelity to routes and wintering areas. Florida Ospreys spent a similar amount of time on their South American wintering areas (146 d, Table 2) when compared with Ospreys migrating from New York and New Jersey (153 d) or Minnesota (160 d; Martell et al. 2001). However, Florida Ospreys arrived on their South American territories between the beginning of August and mid-September, ahead of the more northerly breeding birds that are just beginning their fall migration at this time. Moreover, Florida Ospreys began their return migration in January, which is well before any northern breeding Ospreys initiate northward movements (Martell et al. 2001).

Not all southern Florida Ospreys migrate to South America. Some move off their breeding areas to nonbreeding sites in Florida, while others remain on their breeding areas year round. Partial migration occurs in other avian species (Cristol et al. 1999) including some where the ratio of migrants to non-migrants changes with latitude (Henny 1972). No other Osprey population along the eastern seaboard appears to be non- or partially

migratory (Henny and Van Velzen 1972; Poole and Agler 1987).

Many questions remain regarding the migrating habits of South Florida Ospreys including possible differences between genders, age groups, and the effects of successful versus unsuccessful breeding. Data from other Osprey populations suggest that migratory behavior remains constant from year to year, but further observation of this population is warranted to determine if the same holds true in Florida. The extent to which northern breeders use Florida also needs to be examined in more detail, especially with respect to interactions of wintering birds, with local breeders.

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ELEVATED LEAD LEVELS IN URBAN HOUSE SPARROWS: A THREAT TO SHARP-SHINNED HAWKS AND MERLINS?

RICHARD B. CHANDLER, ALLAN M. STRONG,¹ AND CARLIN C. KAUFMAN
*University of Vermont, School of Natural Resources, Wildlife and Fisheries Biology Program,
Burlington, Vermont 05405 U.S.A.*

ABSTRACT.—In urban environments, lead (Pb) has been recognized as a health threat to humans as well as wildlife. Although this hazard has waned since the banning of leaded gasoline and paint in the 1970s, soil and atmospheric Pb concentrations have remained higher in disturbed habitats than in exurban habitats. Our study evaluated the threat of Pb exposure to Sharp-shinned Hawks (*Accipiter striatus*) and Merlins (*Falco columbarius*) by measuring blood Pb concentrations of the House Sparrow (*Passer domesticus*), a favored prey species and a Eurasian exotic with a history of elevated Pb levels. In 2002, we found blood Pb concentrations of urban House Sparrows in Vermont, U.S.A., were significantly (4.5-fold) greater than in an agricultural control group. Because urban-dwelling Sharp-shinned Hawks and Merlins both selectively prey upon House Sparrows, they may be accumulating Pb. Analysis of 1970–2002 Christmas Bird Count data confirmed an increase in wintering Sharp-shinned Hawks in Vermont and found a significant correlation ($r^2 = 0.456$, $P < 0.05$) between the rate of Sharp-shinned Hawk population increase and the mean abundance of House Sparrows. However, House Finch (*Carpodacus mexicanus*) abundance and rate of increase were more strongly related to the Sharp-shinned Hawk increase ($r^2 = 0.732$, $P < 0.001$ and $r^2 = 0.731$, $P < 0.001$; respectively). We found no positive correlation between Sharp-shinned Hawks and two common native New England residents, Black-capped Chickadee (*Poecile atricapilla*) and Purple Finch (*Carpodacus purpureus*), suggesting introduced prey species may partially explain the mechanism behind the “short-stopping” phenomenon occurring in a portion of the Sharp-shinned Hawk’s range. The degree to which the exposure to lead-laden House Sparrows threatens urban raptor populations is unclear, and we recommend a more detailed examination of the contaminant levels in urban-dwelling raptors.

KEY WORDS: *Sharp-shinned Hawk; Accipiter striatus; House Sparrow; Passer domesticus; Merlin; Falco columbarius; lead; migration; Pb; urban ecosystem.*

NIVELES ELEVADOS DE PLOMO EN GORRIONES CASEROS URBANOS: ¿UNA AMENAZA PARA LOS GAVILANES Y LOS HALCONES PALOMEROS?

RESUMEN.—En los ambientes urbanos, el Plomo (Pb) ha sido reconocido como una amenaza para la salud humana y de la vida silvestre. Aunque este peligro ha disminuido desde la prohibición de la gasolina y pinturas con plomo en los 70’s, las concentraciones de plomo en el suelo y la atmósfera han permanecido más altos en hábitats alterados que en hábitats al exterior de las urbes. Nuestro estudio evaluó la amenaza por exposición a plomo de los gavilanes (*Accipiter striatus*) y los halcones palomeros (*Falco columbarius*) a través de la medición de las concentraciones de plomo en la sangre de gorriones caseros (*Passer domesticus*), una presa predilecta, además de ser una especie exótica Euroasiática con una historia de elevados niveles de plomo. En el 2002, encontramos que las concentraciones de plomo en la sangre de gorriones urbanos en Vermont, U.S.A., fueron significativamente (4–5 veces) más grandes que en un grupo control ubicado en una zona agrícola. Debido a que los gavilanes y halcones palomeros que habitan zonas urbanas depredan selectivamente sobre los gorriones caseros, pueden ellos estar acumulando plomo. El análisis de los datos de los conteos navideños de aves de 1970–2002 confirman un incremento de los gavilanes invernantes en Vermont y encontramos una correlación significativa ($r^2 = 0.456$, $P < 0.05$) entre la tasa de incremento de la población de gavilanes y la abundancia media de gorriones caseros. Sin embargo, la abundancia y la tasa de incremento de los pinzones caseros (*Carpodacus mexicanus*) estuvo mas fuertemente relacionada al incremento de los gavilanes ($r^2 = 0.732$, $P < 0.001$ y $r^2 = 0.731$, $P < 0.001$; respectivamente). No encontramos correlaciones positivas entre los azores

¹ E-mail address: allan.strong@uvm.edu

y dos aves nativas, residentes comunes de New England, los paros de gorra negra (*Poecile atricapilla*) y los pinzones purpúreos (*Carpodacus purpureus*), sugiriendo que las especies presa introducidas pueden explicar parcialmente el mecanismo que se encuentra detrás del fenómeno de “parada corta” que ocurre en una porción del rango del gavilan. El grado en el cual la exposición a gorriones caseros cargados con plomo amenaza a las poblaciones de rapaces urbanas, no es claro y recomendamos un examen más detallado de los niveles de contaminantes en las rapaces que habitan en las urbes.

[Traducción de César Márquez]

Urban ecosystems are highly-modified landscapes characterized by severe disturbances and high proportions of introduced species (Beisinger and Osborne 1982, Gilbert 1989, Blair 1996). These ecosystems are circulation and accumulation sites for a suite of environmental contaminants including lead (Pb), a toxic trace metal remaining in street dust and soils from the leaded gas era and from the use of leaded paints (de Eduardo et al. 1997). Typically, urban ecosystems do not provide high-quality habitat for most wildlife species as evidenced by low species richness (Beisinger and Osborne 1982, Blair 1996); however, as cities, towns, and agricultural expansion have impacted the natural landscape, new or modified niches have arisen. Within the United States, many native wildlife species from a variety of taxa are adapting to human-modified ecosystems and, in certain cases, have become successful at exploiting these new niches. Raptors such as Merlins (*Falco columbarius*), Peregrine Falcons (*Falco peregrinus*), Red-tailed Hawks (*Buteo jamaicensis*), Cooper's Hawks (*Accipiter cooperii*), Mississippi Kites (*Ictinia mississippiensis*), and Eastern Screech-Owls (*Otus asio*) have altered their habitat use patterns to take advantage of urban resources (DeMent et al. 1986, Sodhi and Oliphant 1993, Viverette et al. 1996, Boal and Mannan 1999, Kaplan 2000, Berger 2001).

Although these cases suggest successful adaptation to urban environments, the costs to raptors in urban ecosystems have not been fully evaluated. Boal and Mannan (1999) illuminated a few of the environmental threats facing urban Cooper's Hawks, but they focused primarily on human activity around nests, automobile collisions, and diseases. Other sublethal effects may also counteract short-term population increases. In this study, we examined the potential toxicological threat posed by elevated Pb levels in a common, synanthropic prey species, the House Sparrow (*Passer domesticus*). House Sparrows were chosen as a focal species because they are a preferred prey item for Merlins and Sharp-shinned Hawks (*Accipiter striatus*) in developed landscapes (Sodhi and Oliphant 1993,

Dunn and Tessaglia 1994) and we have witnessed several Merlin and Sharp-shinned Hawk attacks on House Sparrows within our study area. Additionally, documentation of elevated Pb levels among urban songbirds (Getz et al. 1977), a Peregrine Falcon that contracted a *Pseudomonas* infection as a result of preying on Rock Doves (*Columba livia*) with elevated Pb levels (DeMent et al. 1986), and the documentation of at least seven species of North American raptors that have died from Pb poisoning (Locke and Friend 1992) warrant further investigation of the role of House Sparrows in Pb accumulation in raptors.

We paid special attention to Sharp-shinned Hawks because of the recently documented “short-stopping” phenomenon, in which a portion of their eastern population has reduced its migration distance and remained in New England throughout the winter (Duncan 1996). This short-stopping appears to explain partially the substantial decreases in numbers of Sharp-shinned Hawks at fall hawk watch sites along the East Coast during the past two decades (Duncan 1996, Viverette et al. 1996) and may be tied to increased prey availability in urban ecosystems. Although the ecological mechanism behind the short-stopping phenomenon has yet to be investigated, if selected urban prey species exhibit higher Pb loads than do exurban prey, Sharp-shinned Hawk populations could face a toxicological risk.

Previous ornithological studies (e.g., DeMent et al. 1986, Sodhi and Oliphant 1993) in urban environments and our observations of raptors in urban regions of Vermont led us to the prediction that House Sparrows may pose a toxicological threat to urban Sharp-shinned Hawks and Merlins. Consequently, we examined the following hypotheses: (1) a portion of the Sharp-shinned Hawk population has shifted its migratory behavior in response to the increased food availability associated with human-modified environments, and (2) in urban areas, Pb continues to be a threatening trace element to wildlife, persisting in some avian food chains. Our goal was to determine whether Pb is

persistent in the prey base of these two raptors, and if so, are wintering populations consuming House Sparrows affected by potential toxicological threats?

METHODS

We analyzed Christmas Bird Count (CBC) data from 1970–2002 in 11 of 18 Vermont count circles (National Audubon Society 2002). These 11 circles represent all those with data from at least 1975, the first year of Duncan's (1996) analysis of the Sharp-shinned Hawk short-stopping phenomenon. Vermont was selected as a representative study region in New England because its wintering Sharp-shinned Hawk population has increased significantly (Duncan 1996). In Vermont, Merlin populations are not large enough in winter to analyze using CBC data. The mean annual rate of Sharp-shinned Hawk population increase was determined for each CBC circle by regressing the number of birds/party hr on count year. Rates of Sharp-shinned Hawk increase were regressed on mean abundances and mean annual rates of change of House Sparrows and three reference species: House Finches (*Carpodacus mexicanus*), Purple Finches (*Carpodacus purpureus*) and Black-capped Chickadees (*Poecile atricapilla*), with each CBC circle assumed to be an independent data point. Mean abundance for each CBC circle was calculated as the mean number of individuals encountered (1970–2002)/party hr. This measure allows for relative rather than absolute comparisons of species abundances among CBC circles. Mean annual rates of change were calculated following the same methodology as defined above for Sharp-shinned Hawks.

We selected House Sparrows as a focal species based upon our observations of urban predator-prey interactions, their high abundance in urban areas of New England, and their history of Pb accumulation (Getz et al. 1977). House Sparrows likely accumulate Pb when ingesting grit for digestive purposes (Gionfriddo and Best 1995). This species is also regularly taken by both Merlins and Sharp-shinned Hawks in human modified habitats and falls within the preferred size class of prey taken by both raptors (Lowther and Cink 1992, Sodhi and Olyphant 1993, Dunn and Tessaglia 1994).

Our reference species were all winter residents and recognized prey species of Sharp-shinned Hawks (Bildstein and Meyer 2000). We chose these species because their habitat associations differ from those of House Sparrows, making them appropriate species for evaluating the hypothesis that Sharp-shinned Hawks are short-stopping in response to the abundance of urban exotics. Black-capped Chickadees are a common winter resident in New England associated with natural and human-modified habitats. Purple Finches are generally considered forest dwelling species, although they are also a common visitor to birdfeeders. House Finches are the most synanthropic of the reference species, found in urban and residential areas but are more readily found in suburban areas than House Sparrows (Blair 1996).

Pb concentrations in venous blood are good indicators of acute or chronic environmental exposure as well as of body Pb burden (Reiser and Temple 1981, Hunter 1986). To examine Pb levels in House Sparrows, we collected

blood samples from birds in three locations. Our experimental sites were located in two urban areas in Burlington, Vermont; one in a high-density residential district and the other in the business district. Busy roads and sidewalks were features common to both locations, and within these areas House Sparrows seemed to aggregate around low, dense vegetation. The residential district was a primarily residential neighborhood interspersed with some small businesses. The netting site within the business district was close to a central park, large parking lots, and buildings taller than 10 m. Small convenience stores, banks, and restaurants were more common here than within the residential district. Our reference site was a conventional dairy farm in a rural region of Vermont, approximately 55 km southeast of Burlington. We used mist nets to capture House Sparrows prior to collecting <1 dl of blood from the alar vein of each bird in heparinized capillary tubes from a small puncture made using a 22-gauge needle. The samples were frozen (below -20°C) until analyzed.

All samples were diluted five-fold and analyzed for Pb on a Perkin-Elmer SIMAA 6000 graphite furnace atomic absorption instrument equipped with a transversely-heated furnace, Zeeman background correction, autosampler, and electrodeless discharge lamp. A matrix modifier consisting of ammonium phosphate, Triton X-100, and nitric acid was mixed with all samples. Quality-control samples included a method blank, laboratory control samples, and a standard reference (NIST 955b1, Lead in Bovine Blood). Blood mass was low, preventing analysis of matrix spike or duplicate samples. However, two capillary tubes from the same individual were used as field duplicates, which showed identical blood Pb concentrations. Laboratory Quality Assurance data were acceptable and showed low blank levels and good accuracy. Concentration units are reported in parts per million (mg/l) with a detection limit of 0.005 ppm.

Because of the paucity of information available concerning raptors in urban environments, we have included observations from the field that indicated either modified foraging behaviors or potential threats to these species. All observations were collected opportunistically by the authors on raptors inside Burlington's city limits.

RESULTS

Sharp-shinned Hawks showed significant increases in 9 of 11 Vermont count circles between 1970 and 2002. These rates of change were positively correlated with mean winter House Sparrow abundances ($F = 8.2$, $df = 1, 9$, $P < 0.05$, $r^2 = 0.476$; Fig. 1), though not with House Sparrow mean annual rate of change ($F = 0.171$, $df = 1, 9$, $P > 0.6$, $r^2 = 0.019$). They were inversely correlated with mean abundance of Purple Finches ($F = 6.7$, $df = 1, 9$, $P < 0.05$, $r^2 = 0.4255$); and highly positively related with both mean abundance ($F = 24.5$, $df = 1, 9$, $P < 0.001$, $r^2 = 0.732$; Fig. 2) and mean annual rate of change ($F = 24.4$, $df = 1, 9$, $P < 0.001$, $r^2 = 0.731$; Fig. 2) of House Finches. The Sharp-shinned Hawk population increase was not

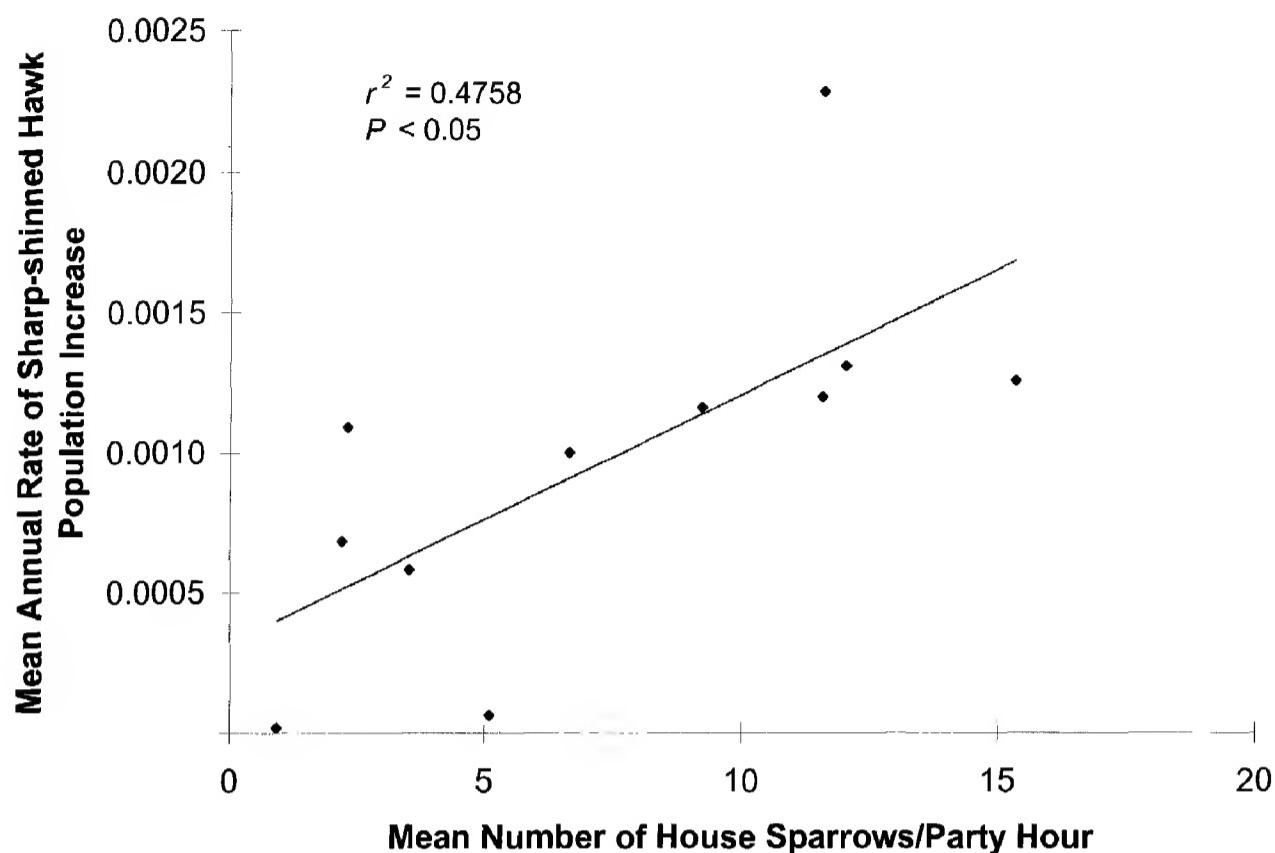


Figure 1. Rate of Sharp-shinned Hawk population change was significantly correlated with abundance of House Sparrows in Vermont Christmas Bird Counts, 1975–2002.

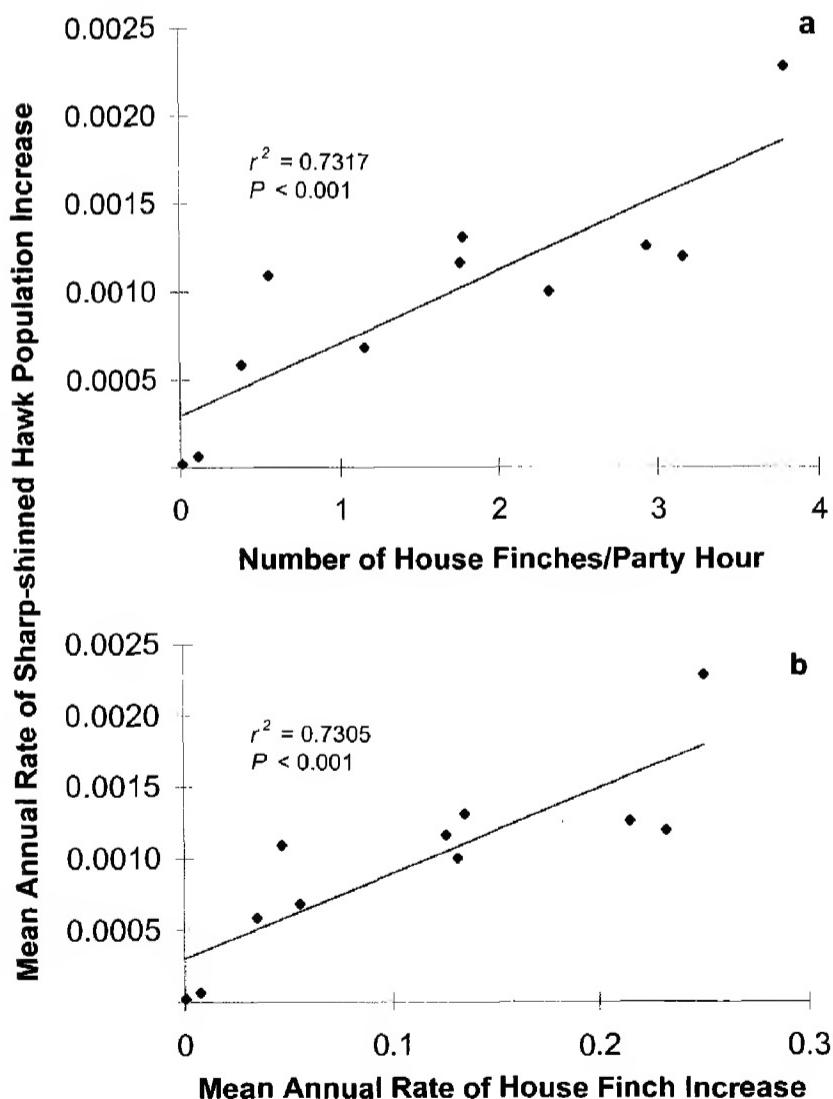


Figure 2. Rate of Sharp-shinned Hawk population change was significantly correlated with abundance (a) and rate of change (b) of House Finches in Vermont Christmas Bird Counts, 1975–2002.

correlated with either abundance or mean annual rate of change in Black-capped Chickadees ($F = 0.1$, $df = 1, 9$, $P > 0.7$, $r^2 = 0.012$; $F = 0.5$, $df = 1, 9$, $P > 0.45$, $r^2 = 0.052$; respectively) or with mean annual rate of change of Purple Finches ($F = 4.9$, $df = 1, 9$, $P > 0.05$, $r^2 = 0.354$).

Blood Pb concentration differed among House Sparrows in the three study groups ($F = 10.16$, $df = 2, 24$, $P < 0.001$; Table 1). We found no difference in Pb concentrations between the two urban groups ($t = 0.873$, $df = 11.7$, $P = 0.40$); therefore, we combined residential district ($N = 8$) and business district ($N = 8$) into a single urban category. Blood Pb concentrations were more than 450%

Table 1. Blood lead concentrations in House Sparrows in Vermont, 2002 varied significantly among three habitats.

LOCATION	N	MEAN BLOOD PB CONCENTRATION ± SD (ppm) ^a
Urban, business district	8	0.083 ± 0.068
Urban, high-density residential district	8	0.108 ± 0.042
Urban combined	16	0.095 ± 0.053
Reference	11	0.021 ± 0.012

^a $F_{2, 24} = 10.16$, $P < 0.001$.

greater in urban ($N = 16$) than agricultural ($N = 11$) House Sparrows ($t = 5.183$, $df = 16.9$, $P < 0.001$). Despite significantly higher blood Pb concentrations, the combined urban mean of 0.0953 ppm is probably not high enough to affect survival or reproductive rates negatively (Getz et al. 1977, Redig 1984). However, we found substantial individual variation, with one individual exhibiting a blood Pb concentration of 0.209 ppm.

Sharp-shinned Hawks, Cooper's Hawks, Merlins, Peregrine Falcons, Red-tailed Hawks, and Bald Eagles (*Haliaeetus leucocephalus*) were all observed within Burlington's urban zone during the winter 2001–02. On five occasions, Sharp-shinned Hawks or Merlins were observed either hunting or feeding upon House Sparrows. We did not observe these two species pursuing prey species other than House Sparrows.

DISCUSSION

Our results provide support for the hypothesis that population increases in wintering Sharp-shinned Hawk populations in Vermont are strongly correlated with prey availability in human-modified environments. Our anecdotal observations of these raptors hunting in urban environments, combined with previous studies showing House Sparrows to be the codominant prey species taken by Sharp-shinned Hawks at birdfeeders (Dunn and Tessaglia 1994) suggest that large House Sparrow populations provide a plausible causal mechanism for the increase of winter raptor populations. Though we did demonstrate that Sharp-shinned Hawks increased proportionally with mean densities of House Sparrows, we found that House Finch abundances and rates of change were more strongly related to changes in raptor numbers. That we found no significant relationship with mean annual rate of House Sparrow increase supports the hypothesis that House Finches were primarily responsible for attracting these hawks into urban and suburban areas. However, we also suggest that House Sparrows are an important food source for raptors within these modified habitats. Merlins in particular are known to feed almost exclusively on House Sparrows, which can comprise more than 70% of prey items taken in urban environments (Sodhi and Olyphant 1993). In fact, in Vermont, there was a strong correlation between the rate of House Finch increase and mean abundance of House Sparrows ($F = 31.8$, $df = 1, 9$, $P < 0.01$, $r^2 = 0.76$). Consequently, raptors that have adapted to these

modified environments may have responded to increasing House Finch populations, which also likely enabled them to exploit abundant, stable House Sparrow populations. Thus, it is plausible that both species of raptors are curtailing their southward migrations to take advantage of the increased introduced prey base.

Theoretical arguments regarding the costs and benefits of migration support our hypothesis. Raptors, like other migratory birds, are believed to depart their breeding grounds in response to the deteriorating conditions brought about by winter climates (Rappole 1995). Because Neotropical migratory songbirds typically comprise the vast majority of Sharp-shinned Hawk's diet (Bildstein and Meyer 2000), it is probable that fall migration of these prey species is the most important reason for this raptor's migration. Assuming migration is a trade-off between breeding season productivity and mortality during migration and the nonbreeding season, it is possible that increased food resources at higher latitudes (e.g., House Sparrows and House Finches) might alter the cost-benefit ratio of migration such that winter mortality at higher latitudes is less than or equal to migration mortality + winter mortality at lower latitudes. Thus, Sharp-shinned Hawks could be expected to increase in areas with high populations of resident prey species. The Black-capped Chickadee and the Purple Finch, two common winter residents in New England, do not appear to be associated with winter population increases of Sharp-shinned Hawks. Rather, our data suggested that House Sparrow and House Finch populations provided the prey base that has led to increased winter populations of Sharp-shinned Hawks in Vermont, as a result of short-stopping migratory patterns. Because of the differences between these prey species' habitat associations, we conclude that the increase in hawks appears to be most rapid in urban and residential areas. The inverse relationship between Purple Finches and Sharp-shinned Hawks may also indicate that the short-stop phenomenon is not occurring in natural habitats.

Our results also showed that blood Pb concentrations were measurable in House Sparrow populations, and compared to rural populations, were ca. 4.5× higher in urban areas (Table 1). Thus, despite the fact that Pb has been banned in gasoline and paint for over 20 yr, environmental sources are still sufficiently abundant to show movement into higher trophic levels. However, this elevated Pb

level was not lethally threatening to House Sparrows, which have been shown to sustain higher concentrations (Getz et al. 1977). It is plausible that sublethal effects might make individuals with elevated blood Pb concentrations more susceptible to predation (Peterle 1991:108).

Although our results showed an increase in Sharp-shinned Hawk populations in areas with high House Sparrow populations and elevated blood Pb concentrations in this prey species, the threat to urban raptors was equivocal. Several toxicity studies of raptors have indicated that in controlled conditions, Pb can biomagnify to threatening or lethal levels when lead-laden prey species were consumed. The infection leading to the death of an urban Peregrine Falcon was contracted as a result of its susceptibility to infection from continual depredation of Rock Doves with blood Pb levels approximately nine times higher ($\bar{x} = 0.901$ ppm) than those found in our study of House Sparrows (DeMent et al. 1986). A controlled toxicological experiment in which a Pb acetate trihydrate solution was administered to nine raptors of three species found that blood Pb levels between 5 and 8 ppm led to clinical signs in five individuals and death in four (Reiser and Temple 1981).

Conflicting information on accumulation rates and effects of lead are common. These discrepancies are typically explained by differences in study design and interspecific variation in susceptibility to Pb (Peterle 1991). Franson et al. (1983), for instance, reported no major physiological effects on American Kestrels (*Falco sparverius*) with blood Pb levels as high as 33 ppm. Wild predatory birds may be affected differently by contamination than captive birds because of differences in metabolic rates and behaviors. For example, predators may not be able to forage as effectively with high contaminant loads (Peterle 1991). The relatively short duration of laboratory experiments also may not reveal sublethal risks posed by long-term Pb exposure. The Peregrine Falcon death also suggested that risk of infectious disease may have increased with increased Pb load, a threat possibly exacerbated in the wild. These factors make it difficult to determine the threat to raptors feeding on House Sparrows with the blood Pb concentrations reported in this paper. Therefore, we suggest that the probability of biomagnification of lead is worthy of further investigation.

Urban raptors may face a significant toxicological threat if, as our data indicate, high levels of

toxins are present in urban prey species and a significant proportion of a raptor population alters its migratory behavior to exploit these prey. The risks of such a scenario is impossible to assess without measuring the actual Pb levels in a population of urban raptors (Newton 1998), and unfortunately no such data have been collected. We also note that Pb levels have not been measured in House Finches. These uncertainties, as well as the lack of knowledge of biologically incorporated Pb intake rates in birds of prey indicate the need for stronger avian bioaccumulation models and more research into urban ecosystems. Data on sublethal physiological, behavioral, and reproductive effects (e.g., Burger 1995) are also needed. We suggest that a study be performed similar to that of Wood et al. (1996), in which thorough toxicological tests are conducted on New England's wintering urban avian communities, especially birds of prey. This would allow for a detailed comparison of contaminant levels in urban and exurban environments. Although Wood et al. (1996) concluded that decreased numbers of migratory Sharp-shinned Hawks could not be explained by toxicological factors, nonmigratory individuals were not sampled in that study; however, this may be the population segment most at risk to increased Pb levels.

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SHORT COMMUNICATIONS

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CONTAMINANT LEVELS, EGGSHELL THINNING, AND PRODUCTIVITY IN SHARP-SHINNED HAWKS IN FUNDY NATIONAL PARK, NEW BRUNSWICK

STEPHEN J. WOODLEY¹

Ecological Integrity Branch, Parks Canada, 25 Eddy Street, Hull, Québec K1A 0M5 Canada

KENNETH D. MEYER

Avian Research and Conservation Institute, 411 N.E. 7 Street, Gainesville, FL 32601 U.S.A.

DAVID ANTHONY KIRK

Aquila Applied Ecologists, Box 87, Carlsbad Springs, Ontario K0A 1K0 Canada

PETER A. PEARCE

Shamrock Terrace, Fredericton, New Brunswick E3B 2S4 Canada

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Many raptor populations were affected detrimentally by organochlorine (OC) pesticides in Europe and North America during the DDT Era (1946–72) and the evidence for this is both compelling and substantial (e.g., Newton 1979, Risebrough 1986). However, it is now widely assumed that OCs are currently having little impact on raptors, except at the local level (Steidl et al. 1991, Jarman et al. 1996), largely because of the recovery of many populations (e.g., Peregrine Falcon [*Falco peregrinus*]; Cade et al. 1988) and restrictions in use of persistent OCs. Recently, toxicologists have focused more on the carbamate and organophosphorus pesticides, implicated in widespread and direct kills of raptors (e.g., Swainson's Hawk [*Buteo swainsoni*], Goldstein et al. 1996, Mineau et al. 1999). Yet many raptors and other avian species are still showing signs of contamination by OCs, and these chemicals, together with other stress factors, may continue to reduce productivity in some populations (Elliott et al. 1996a, 1996b, Johnstone et al. 1996, Dykstra et al. 1998, Elliott and Norstrom 1998).

Dramatic declines in Eurasian Sparrowhawk (*Accipiter nisus*) populations in Britain and elsewhere in Europe, coincident with the widespread use of DDT and the acutely toxic cyclodiene insecticides, and subsequent recovery following the restrictions in use of these chemicals, have been documented (Newton et al. 1986, Newton and Wyllie 1992). The Eurasian Sparrowhawk's ecological

equivalent in the New World, the Sharp-shinned Hawk (*Accipiter striatus*), also declined during the era of the most intensive North American use of DDT (1946–72; Snyder et al. 1973, Kirk 1997, Kirk and Hyslop 1998), following which populations increased (Bednarz et al. 1990, Bildstein and Meyer 2000). From 1985 to the mid-1990s, Sharp-shinned Hawk numbers declined at traditional migration count sites (hawk watches) in eastern North America, but not in the Midwest and West (Laura 1992, Kellogg 1993a, Kerlinger 1993, Viverette et al. 1996, Wood et al. 1996).

One explanation for the declining counts of Sharp-shinned Hawks that occurred at eastern migration sites is reproductive impairment caused by contaminants (Duncan 1996, Viverette et al. 1996, Bildstein and Meyer 2000). Another is that migratory "short-stopping" (i.e., individuals not completing their traditional migratory route) has resulted in decreased counts; supporting this, Christmas Bird Count data shows an increase in numbers of hawks overwintering in areas north of the hawkwatch sites (Duncan 1996, Viverette et al. 1996).

Wood et al. (1996) stressed the importance of concurrent research on contaminant levels and productivity in Sharp-shinned Hawks. Results of analyses of tissues opportunistically collected from Fundy National Park, New Brunswick, during nesting studies from 1979–81 (Meyer 1987) and 1983–87 (Woodley and Meyer 1991) suggested contaminant stress. Many eggs failed to hatch at study nests and chemical analysis revealed that some birds may have had sufficiently elevated concentrations of organochlorines to cause breeding failure. As well, productivity appeared to be impaired compared to studies in other regions. During 1990 and 1991, we systematically collect-

¹ E-mail address: Stephen.Woodley@pc.gc.ca

ed eggs and blood samples from nesting adult Sharp-shinned Hawks and recently fledged young to determine whether organochlorines could contribute to low productivity. Specifically, we ask: (1) Are OC concentrations in eggs at levels that have been documented to cause reproductive failure in other raptor species? (2) Are contaminant levels in body tissues at levels associated with mortality or sufficient to cause reproductive failure? (3) Are there age class differences in contaminant concentrations suggesting age-dependent accumulation of contaminants over time?

METHODS

We conducted this study in 1979–91 in Albert County, New Brunswick ($45^{\circ}30'N$, $65^{\circ}00'W$). This is in the Acadian forest region, composed of a mixture of boreal forest and southern deciduous forest types (Burzynski et al. 1986). As a result of forest harvesting (1825–1948), cyclical infestations of spruce budworm (*Choristoneura fumiferana*), and old-field succession following abandonment by farmers, there are a wide variety of habitat types. Conifer-dominated mixedwoods comprise 30% of all forest types; the main tree species being red spruce (*Picea rubens*), black spruce (*P. mariana*), balsam fir (*Abies balsamea*), yellow birch (*Betula alleghaniensis*), white birch (*B. papyrifera*), red maple (*Acer rubrum*) and sugar maple (*A. saccharum*); (Burzynski et al. 1986). This region provides suitable habitat for Sharp-shinned Hawks.

Consistent with observations elsewhere in Canada, all nests were in forest stands dominated by coniferous trees (Meyer 1987). We found occupied nests mainly by searching for plucking sites (Meyer 1987). We studied 16 Sharp-shinned Hawk nests, all found during the period 1979–91. Of these, 12 were in Fundy National Park and the remainder nearby.

Productivity. We assessed productivity as the mean number of offspring fledged per nest with eggs, or the mean number fledged per successful nest (a nest in which at least one young was fledged). Both measures were contingent on observing nests until the offspring left.

Egg Contents. Between 1979 and 1984 we collected from nests any unhatched eggs for chemical analysis, whereas in 1990–91 we removed one freshly-laid egg randomly from the clutch. We also removed eggshells from nests to analyze contaminant levels in eggshell membranes.

We used calipers to measure egg dimensions and measured eggshell thickness using a Starrett 1010 micrometer (± 0.001 mm; (L.S. Starrett Company, Athol, MA). Egg contents were placed in acetone-washed glass containers, and frozen until transported to the National Wildlife Research Centre, (then in Hull, Québec) for chemical analysis. Eggshells were air-dried for at least 2 wk, and then weighed using a triple-beam balance (± 0.01 g).

We determined shell thickness indices using the formula developed by Ratcliffe (1967): egg shell mass (mg)/length \times breadth (mm). We then calculated percent thinning by comparing this with the pre-1947 thickness index in eggs from southern Canada (mean Ratcliffe thickness index 1.31 ± 0.01 95% CL, $N = 568$; Anderson and Hickey 1972). Ratcliffe indices were derived from

one egg per nest; where there were two eggs, the mean was taken.

Blood Plasma Levels. We sampled blood plasma levels in adult and young hawks at five nests during the breeding seasons (July–August) of 1988, 1990, and 1991. We caught adults using noose carpets on plucking stumps or with Dho gaza nets and a stuffed Great Horned Owl (*Bubo virginianus*) as a decoy. We caught recently-fledged young with bal chatri traps and used live House Sparrows (*Passer domesticus*) as bait. We extracted one milliliter of blood from the brachial vein of each bird, using a 3 ml disposable syringe containing heparin and 26 gauge needle. Blood samples were centrifuged and the plasma stored frozen until analysis.

Residues in Liver Samples. Between 1985 and 1990, we collected 24 hawks killed by collisions with vehicles or windows (New Brunswick, 10; Nova Scotia, 7; Newfoundland, 6; and Prince Edward Island, 1). Hawks were frozen until contaminant analyses were performed; only livers were analyzed for contaminants. Most dead hawks were collected in 1987 (12), followed by 1988 (5), 1986 (4), 1990 (2), and 1985 (1). We classified dead hawks by age and the date they were found: an immature hawk found dead up to 31 December of its first calendar year of life was considered a hatch-year (HY) bird, an immature hawk found dead from 1 January onwards was a second-year (SY) bird, and any adult birds were classed as after second-year (ASY; Canadian Wildlife Service 1977). HY and SY hawks were aged more precisely using 1 July as the mean hatching date in the study area. Carcasses were thawed, livers removed, and standard protocols used for analyses (Peakall et al. 1986).

Contaminant Analyses. Apart from analyses conducted prior to 1984 (by the Ontario Research Foundation), all contaminant analyses were performed at the National Wildlife Research Centre. Standard and strict protocols were used for both laboratories (pre- and post-1984) as described by Peakall et al. (1986). All contaminant concentrations are reported on a wet weight basis; we did not correct for water loss because water content for all eggs was $>70\%$. The detection limit for residues was 0.001 mg/kg.

PCB concentrations are reported as the sum of 41 congeners. Prior to 1988, the sum of PCB congeners was expressed as the 1:1 ratio of Aroclor 1254:1260 (Norstrom 1988). To convert Aroclor 1:1 values to the sum of PCBs, we used a conversion factor based on large numbers of specimens for which Aroclor ratios and total summed PCB congeners were available (Turle et al. 1991). We acknowledge some biases in this technique due to site and species variability.

Diet. To investigate where hawks may be obtaining contaminants, we collected prey remains at plucking posts and nests in 10 territories. We identified prey using a reference collection of beaks, legs, feet, wings, and feathers and by comparison with specimens in the New Brunswick Museum, Saint John, New Brunswick. We classified prey as Neotropical migrants (wintering mainly south of the United States-Mexico border), short-distance migrants (wintering principally in the continental United States), irruptive migrants (which move periodically and nomadically in response to fluctuations in food supply), or year-round residents based on Canadian Wildlife Ser-

Table 1. Organochlorine and PCB residues (mg/kg wet weight) in Sharp-shinned Hawk eggs collected from Fundy National Park, New Brunswick, in 1979–83 and 1990–91.

COMPOUND	1979–83 (N = 2)		1990–91 (N = 7)		
	MEAN ^{a,b}	MINIMUM AND MAXIMUM	MEAN	95% CL	MINIMUM AND MAXIMUM
DDE	7.53	6.2–9.1	7.33	2.69–20.00	1.44–98.08
DDT	0.07	0.06–0.09	0.04	0.02–0.10	0.01–0.43
DDD	0.09	0.09–0.09	0.08	0.04–0.19	0.02–1.36
Mirex	0.31	0.31–0.32	0.19	0.08–0.43	0.06–1.76
<i>p</i> -Mirex	ND ^c	ND ^c	0.01	0.04–<0.01	ND–0.20
Oxychlordane	0.78	0.72–0.85	0.28	0.18–0.45	0.10–0.54
<i>Trans</i> -nonachlor	0.07	0.07–0.07	0.26	0.20–0.49	0.06–0.74
<i>cis</i> -nonachlor	ND	ND	0.02	0.01–0.06	0.04–0.10
Heptachlor epoxide	0.33	0.30–0.37	0.13	0.08–0.23	0.04–0.36
Dieldrin	0.50	0.39–0.64	0.13	0.02–0.89	ND–0.94
HCB	ND	ND	0.01	0.01–0.02	0.01–0.02
Sum PCBs	1.52	1.42–1.63	1.10	0.71–1.70	0.50–2.49
Percent H ₂ O	77.8	77.4–78.9		83.1 ± 0.52 (SE)	81.9–86.0
Percent lipid	6.7	6.1–7.3		5.0 ± 0.54 (SE)	3.2–7.3

^a Mean of two eggs from the same nest.

^b Means are geometric, except for H₂O and percent lipid where they are arithmetic.

^c ND = not detected, i.e., <0.001 mg/kg wet weight.

vice and Breeding Bird Survey (BBS) databases (C. Downes pers. comm.).

Hypotheses and Statistical Analyses. Because we obtained blood plasma opportunistically from adult or young hawks from the same nests, we could not compare age classes or sexes statistically because the data were not independent. However, we hypothesized that contaminant levels in livers would differ according to age class, sex, and geographical location. Specifically, we predicted that: (1) contaminant levels in livers of HY or SY hawks should be lower than in ASY hawks, which had greater exposure both temporally and geographically, and (2) contaminant levels in livers of female hawks should differ from those of males because females excrete lipophilic contaminants in their eggs. To test these relationships, we used ANOVA or paired tests. Because starving birds have metabolized the fat where contaminants bioaccumulate, they should have higher contaminant burdens in their livers than those in good condition. Therefore, to compare contaminant levels in liver tissues among age classes we used an analysis of covariance (ANCOVA), with percent fat as a covariate. Finally, to test whether any geographical differences existed in contaminant levels, we examined the effects of latitude and longitude (converted to decimal degrees) as predictors in a multiple linear regression (both latitude and longitude have been shown to affect contaminant levels; e.g., DeWeese et al. 1986).

Because contaminant data were highly skewed, they were log-transformed. All contaminant means are presented as geometric means with 95% confidence limits unless otherwise stated (Newton and Wyllie 1992, Elliott and Martin 1994). We performed statistical analyses using SAS (SAS Instit. 1990). Sample sizes in this paper vary greatly for different contaminant tissue analyses, and it

was not possible to collect single eggs, or catch adults or young from every nest. Statistical significance was accepted at $P < 0.05$.

RESULTS

Productivity. Mean clutch size was lower in 1979–83 ($2.8 \pm \text{SE } 0.6$) than in 1990–91 (4.1 ± 0.1). Similarly, mean productivity (the number of young fledged from nests with eggs) was lower in 1979–83 (1.3 ± 0.9) than 1990–91 (2.3 ± 0.6). From the nests where hatch frequencies could be determined, a mean of 1.3 ± 0.3 eggs per nest ($N = 4$) did not hatch in 1979–83, whereas in the 1990s no nest had unhatched eggs ($N = 7$). Two nests that failed to produce young in the 1990s had some of the highest shell-thinning indices; however, fledging success was 75% at two other nests with high Ratcliffe indices.

Egg Contents. We found measurable concentrations of 12 commonly reported organochlorine compounds in egg lipid contents (Table 1). Of these, by far the most prevalent was DDE, followed by the sum of PCBs and oxychlordane. One of two eggs collected from nests in the 1980s had DDE levels of 9.12 mg/kg. Although only two of seven eggs exceeded 10 mg/kg in the 1990s, one had extremely high concentrations, 98.08 mg/kg (Ratcliffe index = 13.7%) and the other held 12.84 mg/kg (Ratcliffe index = 18.3%); an additional egg approached the threshold (7.97 mg/kg). Dieldrin levels did not exceed the level of acute toxicity (1 mg/kg), but one egg in the 1980s contained 0.64 mg/kg and two eggs in the

1990s contained 0.94 and 0.67 mg/kg, respectively. Levels of other cyclodienes did not approach levels of acute toxicity (e.g., heptachlor 1.50 mg/kg) and are therefore not reported. Ratcliffe indices (all from 1990/1991) varied from 5.3–18.3% ($N = 7$) below the pre-DDT norm; only one egg had thinning in excess of 15%, the overall mean thinning was 11%.

Blood Plasma Levels. Blood plasma residue levels were much lower than in egg contents as expected. However, the relative concentrations for different compounds showed a similar ranking in plasma to that in egg lipid. Mean concentrations of contaminants were higher in adult males (e.g., DDE 1.40, range = 0.53–2.65, $N = 3$) than adult females (0.08, 0.01–0.69, $N = 2$) in 11 of 12 compounds. In the only case where a direct comparison could be made at the same nest, the adult male had higher blood plasma levels for 9/12 contaminants (the adult female had higher levels of mirex, *trans*-nonachlor, and DDD). Concentrations were also higher in adult males than nestling (e.g., \bar{x} DDE for nestling males 0.04, 0.02–0.08, $N = 3$; \bar{x} PCBs adult males = 0.69, 0.40–1.75; \bar{x} PCBs nestling males = 0.01, 0.01–0.03), and higher in adult females than nestling (\bar{x} DDE for nestling females 0.03, 0.01–0.14).

Residues in Liver Samples. Residue levels in livers were highly variable, with few discernible patterns in relation to age or gender (Table 2). No significant differences existed among age classes according to ANCOVA (no analyses were performed for DDD and *p*-mirex, because too few specimens contained these chemicals in the HY and SY age classes). Only 1/5 HY and 1/7 SY hawks contained measurable levels of *p*-mirex, and only 2/5 HY and 1/7 SY hawks contained DDT. No significant difference was found in DDE levels among age classes. Comparing adults and immatures (HY and SY combined), irrespective of gender, indicated only one significant difference (for *trans*-nonachlor; Mann Whitney *U*-test $Z = 2.452$, $P = 0.01$). The multiple regression analysis indicated that there was no effect of latitude or longitude on levels of any contaminant in livers of hawks.

Prey Remains. Sharp-shinned Hawks preyed on 24 species of birds: 13 Neotropical migrants, 7 short-distance migrants, and 4 resident or irruptive species (Table 3). No significant difference was found in the proportion of Neotropical compared with short-distance migrant prey species ($\chi^2 = 0.259$, $P > 0.1$) or between the proportion that were Neotropical rather than resident species ($\chi^2 = 2.436$, $P > 0.05$). Prey ranged in size from a Golden-crowned Kinglet (*Regulus satrapa*) to a Ruffed Grouse (*Bonasa umbellus*); all prey with a mass >28 g were likely killed by female Sharp-shinned Hawks. Numerically, Neotropical migrants comprised 38.6%, short-distance migrants 34.8%, and resident or irruptive species 3.7%. However, by mass, short-distance migrants were most important (57.9%), followed by Neotropical migrants (23.5%), and lastly resident and irruptive species (18.1%). The most important species by number was

American Redstart (*Setophaga ruticilla*), followed by American Robin (*Turdus migratorius*), Tennessee Warbler (*Vermivora peregrina*), and White-throated Sparrow (*Zonotrichia albicollis*; Table 3). American Robin contributed most by mass, followed by Ruffed Grouse ($N = 1$), White-throated Sparrow, and Hermit Thrush (*Catharus guttatus*; Table 3).

DISCUSSION

Our results demonstrate that Sharp-shinned Hawks in Fundy National Park were contaminated by several organochlorine compounds in the period 1983–91. Not surprisingly, given its persistence and the extent to which it was used, DDE was, by far, the most important. Levels of some other pesticides (e.g., dieldrin) also were moderately high as well.

Were the levels found in our study high enough to cause impaired reproduction? Several eggs in our study contained close to the critical level of 10 mg/kg DDE (Noble et al. 1993 for summaries of critical levels) and one had 98 mg/kg DDE. Contaminant levels in eggs from Fundy National Park were apparently higher than those in southern Ontario (Elliott and Martin 1994) for seven of eight chemicals detected in 1979–83 and five of 12 in 1990–91, although our very small sample sizes limit this comparison.

The blood plasma data suggested that adults had higher contaminant burdens than young, as in other raptors (Bogan and Newton 1977, Henny and Meeker 1981). Adult males also had higher contaminant levels than adult females, perhaps because females could deposit contaminants in their eggs or because they foraged in different habitats and ate different-sized prey (Bildstein and Meyer 2000). For example, males are more likely to prey on small Neotropical migrant Parulidae than are females (Meyer 1987); and these migrants may have higher contaminant loads as a result of spending the boreal winter in Latin America. Plasma contaminant concentrations in adult males were also higher than those reported by Elliott and Shutt (1993).

Where are Sharp-shinned Hawks in Fundy National Park obtaining these contaminants? Several researchers have proposed that hawks accumulate contaminants from prey while spending the nonbreeding season in Central and South America (Elliott and Shutt 1993, Elliott and Martin 1994), as in the Peregrine Falcon (e.g., Johnstone et al. 1996). However, band recoveries from Cape May, NJ and Hawk Mountain, PA demonstrate that hawks breeding in eastern Canada winter in the Atlantic plain of the southeastern United States, and peninsular Florida (Clark 1985, Viverette et al. 1996), whereas hawks migrating through Great Lakes banding stations winter mostly west of the Appalachians and as far south as Central America (Duncan 1985, Evans and Rosenfield 1985, Carpenter et al. 1990).

We propose that Sharp-shinned Hawks in Fundy National Park are accumulating contaminants both from

Table 2. Organochlorine and PCB residue levels (mg/kg) in livers of Sharp-shinned Hawks found dead in Atlantic provinces between 1985–90. Numbers show geometric means with range in parentheses.

COMPOUND	HATCH-YEAR		SECOND-YEAR		IMMATURES ^a (N)		AFTER SECOND-YEAR		ADULTS ^b (N)	
	FEMALE (N)	MALE (N)	FEMALE (N)	MALE (N)	FEMALE (N)	MALE (N)	FEMALE (N)	MALE (N)	FEMALE (N)	MALE (N)
DDE	1.97 (5) (0.42–7.58)	1.03 (3) (0.77–1.24)	4.32 (4) (1.62–17.31)	2.15 (12) (0.42–17.31)	3.82 (5) (1.79–7.97)	1.76 (4) (0.84–3.63)	2.70 (9) (0.84–7.97)			
DDT	<0.01 (2) (ND–0.02)	ND ^c	<0.01 (1) (ND–0.06)	<0.01 (3) (ND–0.06)	<0.01 (3) (ND–0.01)	<0.01 (3) (ND–<0.01)	<0.01 (6) (ND–0.01)			
DDD	0.03 (5) (0.01–0.07)	<0.01 (3) (<0.01–<0.01)	0.08 (4) (0.02–0.78)	0.03 (12) (<0.01–0.78)	0.01 (5) (<0.01–0.05)	0.01 (4) (0.01–0.02)	0.01 (9) (<0.01–0.05)			
Mirex	0.05 (5) (<0.01–0.22)	0.03 (3) (0.02–0.03)	0.06 (4) (0.02–0.34)	0.05 (12) (<0.01–0.34)	0.05 (12) (<0.01–0.34)	0.17 (5) (0.10–0.29)	0.07 (4) (0.04–0.12)	0.11 (9) (0.04–0.29)		
p-Mirex	<0.01 (1) (ND–0.02)	ND	<0.01 (1) (ND–0.05)	<0.01 (2) (ND–0.05)	0.02 (4) (ND–0.05)	0.02 (4) (ND–0.06)	0.01 (4) (0.01–0.02)	0.01 (8) (ND–0.06)		
Oxychlordane	0.09 (5) (0.03–0.45)	0.06 (3) (0.04–0.10)	0.13 (4) (0.05–0.50)	0.09 (12) (0.03–0.50)	0.13 (0.05–0.23)	0.07 (4) (0.04–0.11)	0.10 (9) (0.04–0.23)			
trans-nonachlor	0.03 (5) (<0.01–0.16)	0.03 (3) (0.02–0.05)	0.02 (4) (<0.01–0.48)	0.02 (12) (<0.01–0.48)	0.02 (12) (<0.001–0.01)	<0.01 (5) (ND–0.05)	<0.01 (3) (ND–0.05)	<0.01 (8) (ND–0.05)		
cis-nonachlor	0.01 (5) (<0.01–0.05)	0.01 (3) <0.01 (2)	0.02 (4) (<0.01–0.09)	0.01 (12) <0.01 (4)	0.03 (5) (0.01–0.04)	0.01 (4) (<0.01–0.02)	0.02 (9) (<0.01–0.04)			
Heptachlor epoxide	<0.01 (2) (ND–0.09)	ND	<0.01 (2) (ND–0.59)	<0.01 (4) (ND–0.59)	ND	0.01 (3) (ND–0.08)	<0.01 (3) (ND–0.08)			
Diieldrin	0.02 (5) (<0.01–0.12)	0.03 (3) (<0.01–0.14)	0.03 (4) (<0.01–0.11)	0.03 (12) (<0.01–0.14)	0.02 (5) (<0.01–0.08)	0.02 (4) (<0.01–0.06)	0.02 (9) (<0.01–0.08)			
HCB	0.02 (5) (<0.01–0.21)	0.03 (3) (0.02–0.06)	0.02 (4) (0.01–0.03)	0.02 (12) (<0.01–0.21)	0.03 (5) (0.01–0.07)	0.01 (4) (0.01–0.02)	0.02 (9) (0.01–0.07)			
Total PCBs	0.55 (5) (0.12–3.51)	0.50 (3) (0.34–0.95)	0.71 (4) (0.28–1.74)	0.58 (12) (0.12–3.51)	1.55 (5) (0.73–3.33)	0.38 (4) (0.32–0.53)	0.83 (9) (0.32–3.33)			
Percent Lipid	3.43 ± 0.51 (2.0–4.88)	2.21 ± 0.56 (1.12–3.00)	3.63 ± 0.17 (3.14–3.96)	3.19 ± 0.29 (1.12–4.88)	4.19 ± 0.97 (2.30–5.94)	4.19 ± 0.50 (2.30–6.43)	4.19 ± 0.50 (2.30–6.43)			

^a Immature = hatch year and second year birds.

^b Adults = after second year birds.

^c ND = no data.

Table 3. Frequency of occurrence and percent biomass of prey items identified in 10 Sharp-shinned Hawk territories in the Bay of Fundy National Park, New Brunswick, study area.

PREY SPECIES	NUMBER	PERCENT BY NUMBER	PERCENT BY MASS (mass in g) ^a
Neotropical migrants			
Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>)	1	0.5	0.3 (11.6)
Swainson's Thrush (<i>Catharus ustulatus</i>)	3	1.6	2.4 (32.7)
Gray Catbird (<i>Dumetella carolinensis</i>)	1	0.5	0.9 (37.2)
Red-eyed Vireo (<i>Vireo olivaceus</i>)	3	1.6	1.4 (18.9)
Tennessee Warbler (<i>Vermivora peregrina</i>)	15	7.9	4.8 (12.9)
Magnolia Warbler (<i>Dendroica magnolia</i>)	6	3.2	1.4 (9.6)
Cape May Warbler (<i>D. tigrina</i>)	3	1.6	0.8 (11.0)
Black-throated Green Warbler (<i>D. virens</i>)	3	1.6	0.7 (8.8)
Blackburnian Warbler (<i>D. fusca</i>)	9	4.8	2.2 (9.8)
Bay-breasted Warbler (<i>D. castanea</i>)	3	1.6	0.4 (15.0)
American Redstart (<i>Setophaga ruticilla</i>)	21	11.1	4.7 (9.1)
Ovenbird (<i>Seiurus aurocapillus</i>)	4	2.1	2.2 (22.7)
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	1	0.5	1.1 (45.6)
Short-distance migrants			
Winter Wren (<i>Troglodytes troglodytes</i>)	5	2.6	1.1 (8.9)
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	1	0.5	0.2 (6.2)
Hermit Thrush (<i>Catharus guttatus</i>)	10	5.3	7.2 (29.1)
American Robin (<i>Turdus migratorius</i>)	18	9.5	34.4 (77.3)
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	10	5.3	3.0 (11.9)
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	14	7.4	8.3 (23.8)
Dark-eyed Junco (<i>Junco hyemalis</i>)	8	4.2	3.9 (19.6)
Irruptive species			
Evening Grosbeak (<i>Coccothraustes vespertinus</i>)	1	0.5	1.3 (54.0)
Year-round residents			
Ruffed Grouse (<i>Bonasa umbellus</i>)	1	0.5	14.2 (576.5)
Downy Woodpecker (<i>Picoides pubescens</i>)	3	1.6	2.0 (27.0)
Boreal Chickadee (<i>Poecile hudsonicus</i>)	2	1.1	0.5 (9.8)
Unidentified warbler	27	14.3	
Unidentified sparrow	14	7.4	
Mammals			
Red-backed Vole (<i>Clethrionomys gappperi</i>)	1	0.5	0.6 (24.0) ^b

^a Masses (g) are from Dunning (1993); where male and female masses were given separately a mean was taken.

^b Mass taken was average of range given by Banfield (1974).

their breeding grounds, and their wintering areas in the southern United States. DDT use was once widespread in North America, and low-level use continues in Mexico, Central and South America (UNEP 2002). Interestingly, New Brunswick forests were subjected to probably the longest and most intensive aerial pesticide spraying program in the world in order to control outbreaks of spruce budworm (Environment Canada 1989). Between 1952 and 1990, 100 000 mt (220 million pounds) of DDT and Fenitrothion were applied and a total of 19.392 million ha were sprayed between 1975 and 1986 (Environment

Canada 1991). Thus, Sharp-shinned Hawks and their prey could be accumulating contaminants from multiple sources.

Unfortunately, we lack data on contaminant levels in prey species of Sharp-shinned Hawks in Fundy National Park. Neotropical migrant songbirds were the most important prey identified in this study. Migrant songbirds have been documented to be contaminated by several OC pesticides (Mora and Anderson 1991, Harper et al. 1996) and DDE levels were generally higher in these species than short-distance migrants or residents (DeWeese

et al. 1986). Five of the species preyed on by hawks in Fundy were shown to contain detectable OC residues (at the ng/g level) by Harper et al. (1996), including Gray Catbirds (*Dumetella carolinensis*), Swainson's Thrushes (*Catharus ustulatus*), Red-eyed Vireos (*Vireo olivaceus*), Bay-breasted Warblers (*Dendroica castanea*), and American Redstarts (*Setophaga ruticilla*). Moreover, American Robins, by far the most important prey item by mass of Sharp-shinned Hawks in our study, have been found to contain extremely high levels of DDE at "hot spots," particularly orchards, elsewhere in Canada (e.g., Elliott et al. 1994, Hebert et al. 1994).

Given our small sample sizes it is difficult to say whether contaminants are having an adverse effect on Sharp-shinned Hawk populations in our study area, or in the Atlantic region generally. However, eggshell thinning in this study was sufficient to cause reproductive failure in at least three of nine (33%) nests. In the Eurasian Sparrowhawk, DDE levels of 62–104 ppm (lipid weight basis) caused shell-thinning of 11–20% and a corresponding population reduction of 14–35%. Productivity in this species was reduced by 14% at 8% thinning and 32% at 20% thinning (Newton et al. 1986). Thus, contaminants merit serious attention by researchers as a possible contributory factor in eastern Sharp-shinned Hawk declines.

RESUMEN.—Entre 1979 y 1984, los gavilanes (*Accipiter striatus*) del Parque Nacional Fundy (New Brunswick) tuvieron un éxito reproductivo bajo en comparación con cualquier otra parte de Norteamérica. Examinamos los parámetros reproductivos de 16 nidos entre 1979 y 1991. Colectamos huevos sin eclosionar, seleccionando aleatoriamente un solo huevo, tomamos muestras de sangre de gavilanes adultos y jóvenes, al igual que muestras de sangre e hígado de la mayoría de los azores muertos en época no reproductiva para analizar sus contaminantes. El adelgazamiento del cascarón varió de 5.3–18.3% bajo la norma anterior a 1947, el rango superior fue más grande que el nivel mínimo de 15% en el cual fracasan en su intento reproductivo otras poblaciones de aves rapaces. Los huevos contuvieron cantidades detectables de residuos de 12 contaminantes comúnmente analizados; el DDE fue el más abundante seguido por los bifenilos policlorados (PCBs). No se encontraron diferencias geográficas en el nivel de contaminantes en los hígados de los azores muertos, no hubo diferencias entre las clases de edad o sexo. Encontramos 24 especies de presas en la dieta de 10 nidos de los azores; los emigrantes neotropicales fueron los más importantes en número, seguidos por los emigrantes de distancias cortas.

[Traducción de César Márquez]

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A RETROSPECTIVE STUDY OF MORTALITY AND REHABILITATION OF RAPTORS IN THE SOUTHEASTERN UNITED STATES

SARA RESS¹ AND CRAIG GUYER

Department of Biological Sciences, Auburn University, AL 36849 U.S.A.

KEY WORDS: *Injury; mortality factor; raptor; rehabilitation; release.*

Increasing habitat loss and fragmentation create more opportunities for humans and raptors to interact, often negatively affecting the birds. As a result, there is a need for rehabilitation facilities that can receive injured ani-

mals, treat wildlife, and release them back into the wild. In this paper we evaluate the effect that humans have on raptors by summarizing records of birds admitted to a raptor rehabilitation center. The records at these centers are valuable sources of data that provide current information on the animals, aspects of their natural history, and conservation.

We examine the following four questions within this paper: (1) are all raptor species equally likely to be released, (2) is the source of injury related to the likelihood for release, (3) do sources of injury differ between

¹ Present address: Department of Biological Sciences, 632 Science and Engineering, University of Arkansas, Fayetteville, AR 72701 U.S.A.; e-mail address: sress@uark.edu

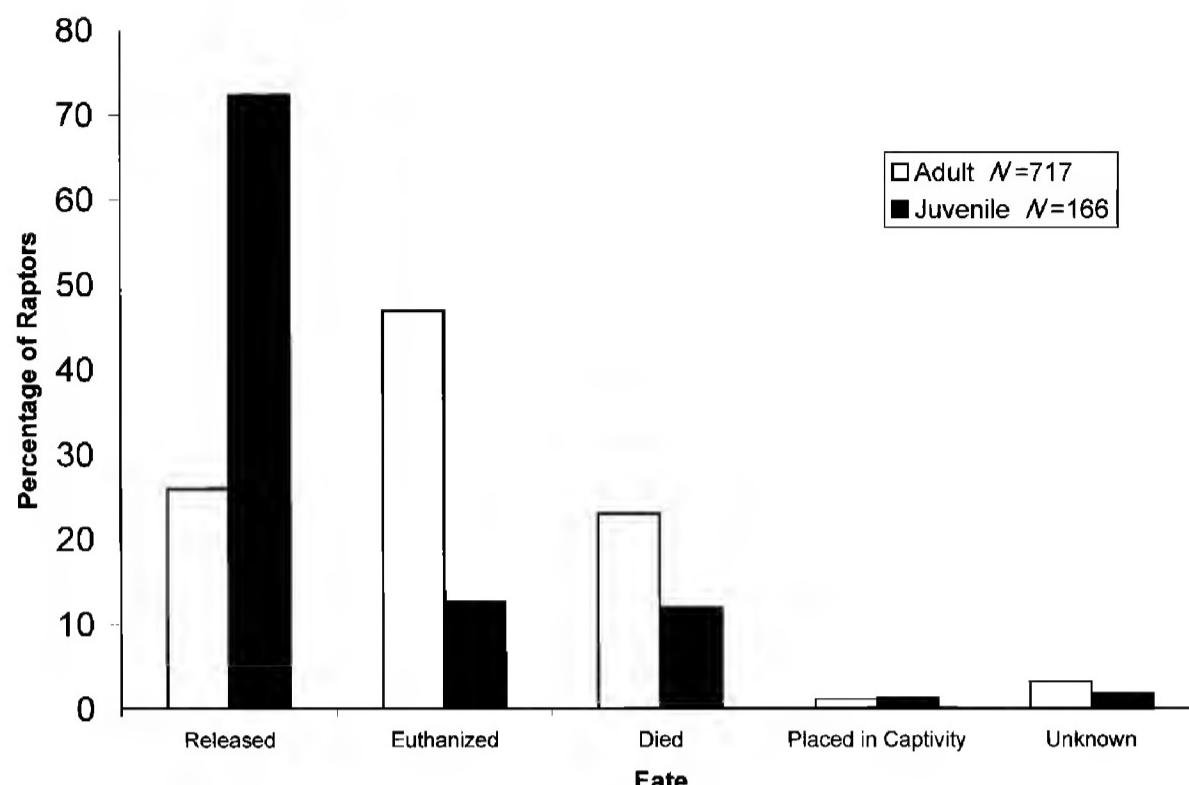


Figure 1. Final fates for raptors admitted to Southeastern Raptor Rehabilitation Center from 1 January 1999–6 December 2000. Unknown column signifies birds that were still retained at the rehabilitation center at the end of the study period. Birds received from falconers and zoos were omitted from analysis.

nocturnal and diurnal species and, (4) does body size affect survival of injured birds? For each question we examined adult and juvenile birds separately.

METHODS

We obtained data from the Southeastern Raptor Rehabilitation Center (SERRC), a facility located in Auburn, Lee County, Alabama. This facility receives injured and juvenile birds of prey from veterinary hospitals, rehabilitators, and other private individuals throughout the southeastern United States and occasionally from beyond this region. All records at SERRC from 1 January 1999–6 December 2000 were evaluated. Species, date admitted, case number, diagnosing injury, cause of injury, and final disposition of each bird were noted. A total of 896 raptors were admitted during this time period. Of these, 13 were omitted from further analysis because they were captive animals admitted from zoos, organizations that used them for educational programs, or by falconers. We then separated the remaining animals ($N = 883$) into two groups: adults, free-ranging animals with hard-pinned flight feathers and no known previous association with humans ($N = 717$), and juveniles, nestling or fledgling birds lacking hard-pinned flight feathers and that either were removed from a nest or found on the ground, presumably near a nest ($N = 166$).

In separate analyses for adults and juveniles, we categorized the causes of injury and determined the percentage of birds that lived or died within each by species. To test whether injury types occurred with equal frequency among all species we used *G*-tests (Zar 1996). For these analyses, the six species of adults with 25 or greater observations and the six species of juveniles with 10 or greater observations were included separately; adults or juveniles of all other species were pooled into a seventh

category for analysis. We performed a second set of *G*-tests by pooling all owls into a single nocturnal-activity category and all hawks into a single diurnal-activity category. The *G*-tests were used to determine whether injury types were distributed equally between the two activity categories for adults and juveniles. Finally, we used linear regression to examine the effects of adult body size on survival. For each statistical test alpha was set at 0.05.

RESULTS

Adults were less likely than juveniles to be released ($\chi^2 = 122.1$, df = 1, $P < 0.0001$; Fig. 1). Because animals donated to educational programs or retained by SERRC were deemed not suitable for release in the wild, we assumed that all of these birds plus those that were euthanized could not have survived; all released birds were considered to have survived their injuries. Therefore, the probability of death was 7.6× higher for adults than juveniles. For adults, there was a significant difference among species in their ability to survive ($\chi^2 = 20.7$, df = 6, $P = 0.002$). This resulted because Eastern Screech-Owls (*Otus asio*), Great Horned Owls (*Bubo virginianus*), and Cooper's Hawks (*Accipiter cooperii*) were all more likely to survive injury than were Red-tailed Hawks (*Buteo jamaicensis*), Barred Owls (*Strix varia*), Red-shouldered Hawks (*Buteo lineatus*), and the category containing the rarer species. We found no significant difference among species in the ability of juveniles to survive ($\chi^2 = 8.5$, df = 6, $P = 0.20$).

Of 19 different causes of injury to adult birds (plus unknown causes), we considered the five most common causes (hit by vehicle, collision/trauma, gunshot, barbed

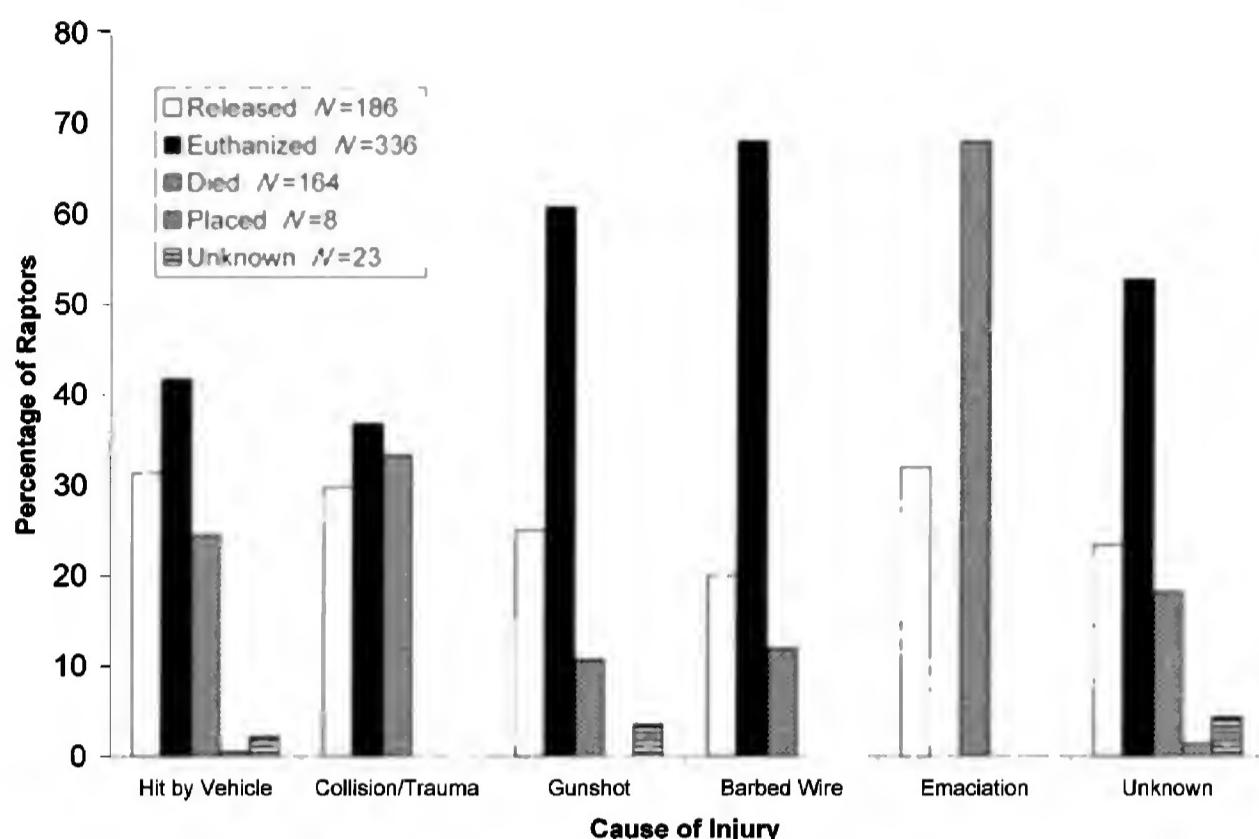


Figure 2. Cause of injuries to adult raptors admitted—Southeastern Raptor Rehabilitation Center from 1 January 1999–6 December 2000.

wire, emaciation) separately and pooled the rest into a single category of other causes for statistical analyses. Birds with unknown outcomes were omitted from consideration. The type of injury did not affect survival rates of birds ($\chi^2 = 5.2$; $df = 5$; $P = 0.38$; Fig. 2). Data were insufficient to determine whether the cause of an injury

played a significant role in determining whether a juvenile lived or died.

Diurnal adult birds had a much higher incidence of gunshot injuries and were slightly more likely to collide with windows than were nocturnal birds ($\chi^2 = 42.3$, $df = 4$, $P < 0.0001$; Fig. 3). Additionally, body size and survi-

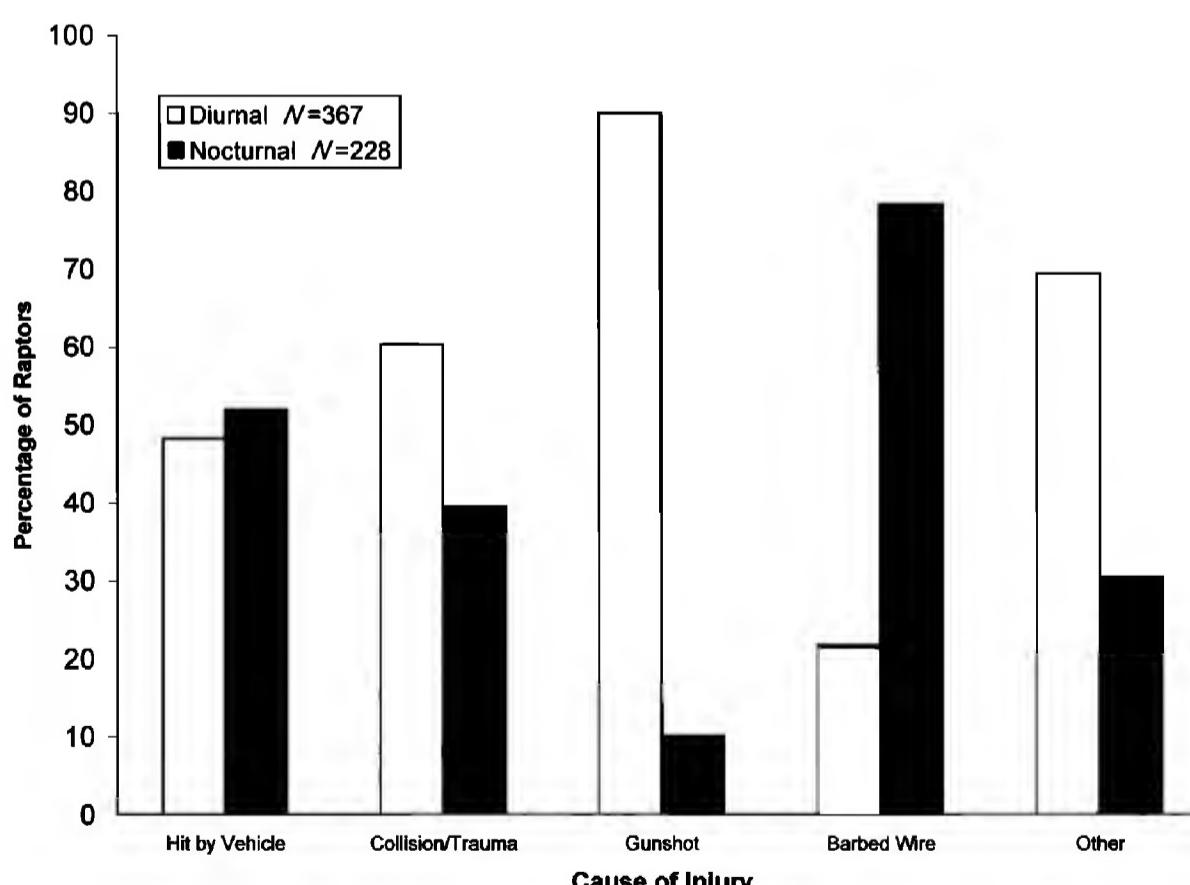


Figure 3. Effect of temporal activity on cause of injury of adult raptors processed by Southeastern Raptor Rehabilitation Center from 1 January 1999–6 December 2000. Birds admitted as a result of an unknown cause were omitted.

vorship of adults were negatively correlated ($R^2 = 0.85$, $df = 4$, $P = 0.026$; Survival = -0.018 [mass] + 45.88). For juveniles, there was no association between activity type (diurnal versus nocturnal) and type of injury ($\chi^2 = .35$, $df = 4$, $P = 0.99$).

DISCUSSION

Our results suggest that activity patterns and body sizes of raptors in the southeastern United States are factors influencing the severity of injuries experienced by these birds. The overall degree of trauma experienced by nocturnal birds appears to be reduced (32.1% survival) relative to diurnal ones (22.6% survival). Similarly, small birds experience reduced trauma relative to large ones. Large, diurnal species are likely to be easier targets for certain injury types (e.g., gunshots), less maneuverable in escaping others (e.g., vehicles), and more prone to increased trauma due to greater inertia when hitting objects. Small, nocturnal species may have lower risks by being more difficult targets, more maneuverable in avoiding objects, and carrying less inertia when they do collide with objects. The pair of birds in our study that did not fit this overall pattern included Great Horned Owls (large bird with high survival) and Barred Owls (nocturnal bird with low survival). These two species differed principally in the greater frequency of collisions and greater variety of injury types experienced by Barred Owls. We suggest that additional data on mortality patterns will eventually demonstrate that some types of injury experienced largely by diurnal birds (e.g., gunshots), to be more severe than other injury types, resulting in higher mortality in these birds than nocturnal ones. Additionally, we suggest that behavioral differences (e.g., foraging strategy) of some nocturnal birds, like Barred Owls, may increase mortality relative to levels experienced by other nocturnal birds.

We found that survival of juveniles of all species is uniform and that this age group is released greater than 50% of the time at one large rehabilitation center. Juveniles typically are taken from nests rather than being found injured, and therefore, the primary rehabilitation goal is to feed and care for them until they are ready for independence. Our data indicate that juveniles of all species are equally responsive to the care given by SERRC. Because adults of these same species did not survive as well, we suggest that this is likely due to their ability to recover from injury and not to their propensity to accept care from humans.

Our results differ from those of Duke et al. (1981), who noted that hawks had higher release rates than owls, and that bird size had no effect on rehabilitation or release success. Similarly, our results do not agree with those of Fix and Barrows (1990), who found no significant difference among species in the occurrence of traumatic injuries. The conclusions reported documented in these studies suggest that the types of injuries experienced by birds differ among regions of the United States.

Factors associated with road density, hunter training, local attitudes toward birds of prey, and habitat features might be important in explaining such trends.

Despite differences among published accounts, an overall pattern emerges from studies of records from raptor rehabilitation centers. These studies document that 21–30% of adult birds admitted to such facilities are released (Duke et al. 1981, Fix and Barrows 1990, Deem et al. 1998) and that most sources of injury are of anthropogenic origin (Keran 1981, Fix and Barrows 1990, Fransson et al. 1996, Sweeney et al. 1997, Deem et al. 1998). One justification for rehabilitation efforts is that released birds represent animals that otherwise would have died. To understand how the release of rehabilitated raptors might contribute to the long-term conservation of raptor populations, much additional information is required.

RESUMEN.—Examinamos los registros que enumeraban las causas de lesión y la disposición final de 20 especies de rapaces (896 individuos) en el Centro de Rehabilitación de Rapaces del Sur oriente en Auburn, Alabama. Estos datos son de 1 enero 1999 al 6 diciembre 2000. Las aves adultas y los juveniles (polluelos o aves que estaban emplumando y carecían de plumas de vuelo endurecidos) se consideraron por separado. A la mayoría de adultos les fue aplicada la eutanasia, mientras que la mayoría de juveniles fueron liberados. Las especies liberadas en mayores ocasiones fueron el búho chirreador oriental (*Otus asio*) (44.6%), seguido por el gavilán de Cooper (*Accipiter cooperii*) (37.8%), el gran búho cornudo (*Bubo virginianus*) (31.1%), y la lechuza de campanario (*Tyto alba*) (30.4%). En los juveniles, todas las especies tuvieron igual oportunidad de ser liberadas.

La causa principal de las lesiones en las aves adultas admitidas fue la colisión con vehículos (26.8%; excluyendo las heridas de origen desconocido). Esta y otras lesiones causadas por el hombre generalmente terminaron en la práctica de la eutanasia mientras que otras aves murieron (71.1%; $N = 804$). La mayoría de los juveniles recibidos también fueron heridos por eventos de origen humano. La causa de las lesiones en los adultos variaron dependiendo si eran especies diurnas o nocturnas; la hora de la actividad no tuvo efecto sobre el tipo de lesiones de los juveniles. En las aves adultas, las más pequeñas fueron liberadas con más frecuencia que las aves grandes. Este patrón no ocurrió con las aves juveniles.

[Traducción de César Márquez]

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BALD EAGLES CONSUME EMPEROR GEESE DURING LATE-WINTER IN THE ALEUTIAN ARCHIPELAGO

MARK A. RICCA¹

U.S. Geological Survey, Western Ecological Research Center, 1 Shields Avenue, University of California, Davis, CA 95616 U.S.A.

ROBERT G. ANTHONY

U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Corvallis, OR 97331 U.S.A.

JEFFREY C. WILLIAMS

U.S. Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge, Aleutian Islands Unit, 2355 Kachemak Bay Drive, Homer, AK 99603 U.S.A.

KEY WORDS: *Bald Eagle*, *Haliaeetus leucocephalus*; *Emperor Goose*, *Chen canagica*; *food habits*; *Alaska*; *Aleutian Archipelago*.

Emperor Geese (*Chen canagica*) are a species of concern because their population has declined rapidly since the mid-1960s and continues to remain below management objectives (Petersen et al. 1994). Emperor Geese are restricted primarily to Alaska and exhibit an east-west migration pattern, whereby most birds begin breeding on the Yukon-Kuskokwim Delta by mid-May, stage on the Alaska Peninsula by late September, and migrate westward to winter in the Aleutian Archipelago from late November to mid-April (Eisenhauer and Kirkpatrick 1977, Petersen et al. 1994). Demographic and movement studies have been conducted on breeding grounds and staging areas (e.g., Schmutz et al. 1994, 1997); however, the

winter ecology of Emperor Geese is poorly understood due in part to the extremely remote nature of the Aleutian Archipelago (Petersen et al. 1994).

Bald Eagles (*Haliaeetus leucocephalus*) are ubiquitous, year-round residents throughout the most of the Aleutian Archipelago (Murie 1959) and obtain most of their prey from the nearshore marine environment (Anthony et al. 1999). We predict that Bald Eagles should prey on wintering Emperor Geese if available because eagles depredate other species of geese in southern latitudes (Frenzel and Anthony 1989, Watson et al. 1991, McWilliams et al. 1994). However, the existing information on Bald Eagle predation of Emperor Geese appears contradictory. Sherrod et al. (1976) suggested geese may be too large for Bald Eagles to kill efficiently, and other studies rarely reported Emperor Geese as Bald Eagle prey in the Aleutians (Murie 1940, White et al. 1971, Sherrod et al. 1976). Conversely, Eisenhauer and Kirkpatrick (1977) stated that Bald Eagles are perhaps the dominant avian predator of wintering Emperor Geese, and cite the observa-

¹ Email address: mark.ricca@usgs.gov

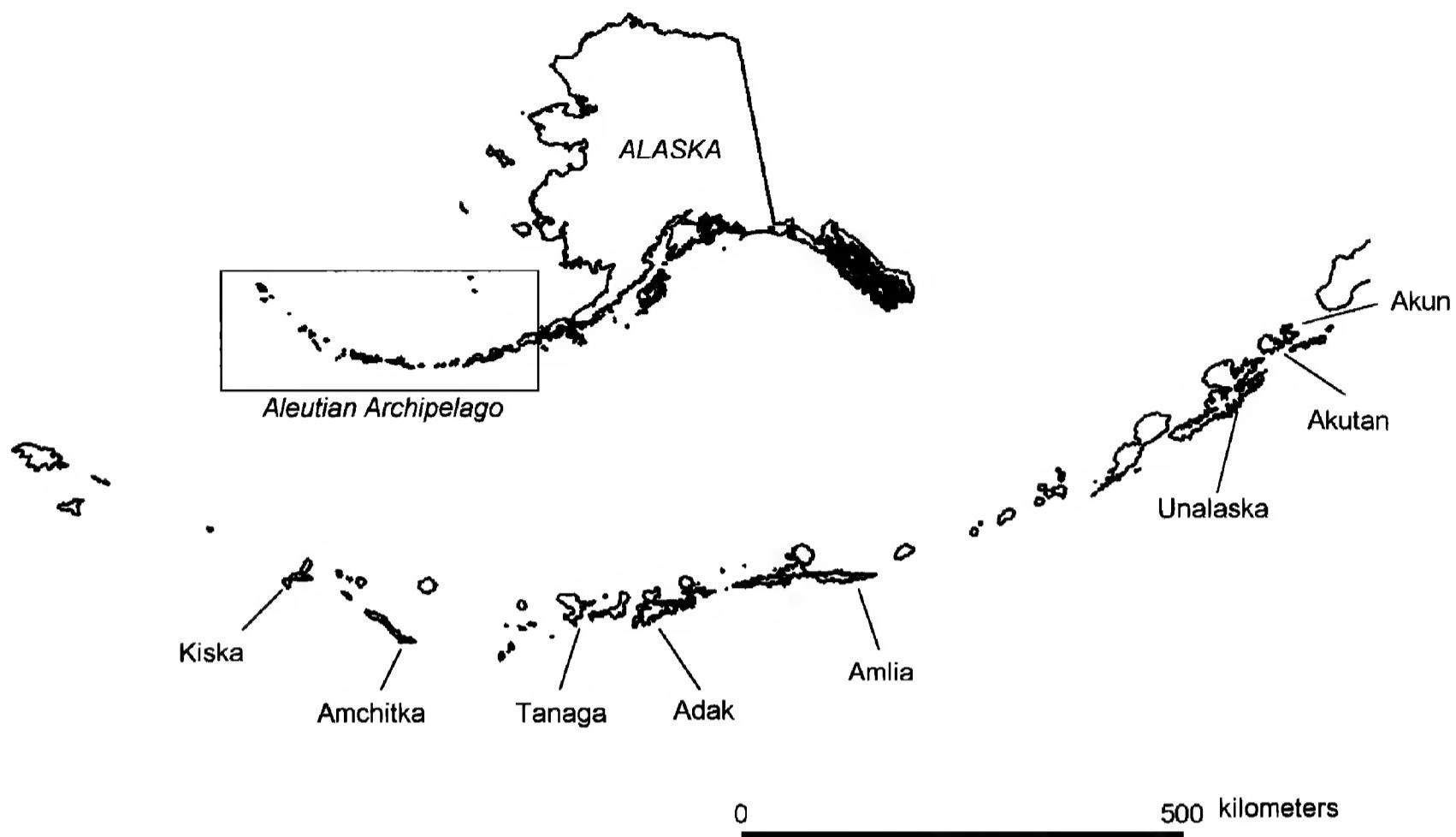


Figure 1. Map of the Aleutian Archipelago indicating islands where Bald Eagle nest surveys occurred, April–May 2000–01.

tions of Williamson et al. (1975) of frequent eagle predation of Emperor Geese on Amchitka Island in the western Aleutian Archipelago. Furthermore, Gill and Kincheloe (1993) observed Bald Eagles depredating Emperor Geese on the Alaska Peninsula. Because almost the entire population of Emperor Geese winters in the Aleutian Archipelago, a need for information on sources of winter mortality exists (Gill and Kincheloe 1993). Emperor Geese have relatively low overwinter survival compared to other goose species, which may play a pivotal role in their demography (Schmutz et al. 1994, 1997). Herein, we describe Bald Eagle diets and the occurrence of Emperor Geese remains in Bald Eagle nest sites during late winter–early spring.

METHODS

We surveyed nesting eagles on Unalaska, Akutan, and Adak islands from 15 April–3 May 2000, and Amlia, Adak, Tanaga, Amchitka, and Kiska from 20 April–28 April 2001 (Fig. 1). We surveyed ca. 1150 km of shoreline from inflatable skiffs with at least two observers visually searching for nesting eagles. Our surveys coincided roughly with the onset of Bald Eagle egg laying (Sherrod et al. 1976) and the end of the Emperor Goose overwintering period (Eisenhauer and Kirkpatrick 1977). We searched a maximum of 16 climbable nests per island. We searched for prey remains in and around nests and recorded the minimum number of individual prey items (Mollhagen et al. 1972, Anthony et al. 1999). We only

counted prey remains from occupied nests that appeared to be from the current year's nesting attempt, which excluded remains that appeared obviously weathered and deeply soiled. We identified most unknown prey remains by comparison with museum specimens housed at the Alaska Maritime National Wildlife Refuge, Adak, AK.

We calculated the percent of Bald Eagle nests containing prey remains, and then the percent of those nests containing Emperor Goose remains by island and year. We estimated Bald Eagle diets by dividing the minimum number of prey items for each prey taxa by the total number of prey items across all islands and years.

RESULTS

We visited 94 Bald Eagle nests during the course of our study. Sixty percent ($N = 18$) of these nests contained prey during 2000, and 89% ($N = 57$) during 2001. No Bald Eagle nests with prey remains contained any identifiable Emperor Goose remains during 2000. However, 39% ($N = 22$) of nests with prey remains contained identifiable remains of Emperor Geese during 2001. Emperor Geese were most frequent (eight of 15 nests) on Kiska, which was the most western island sampled in our study. Emperor Geese occurred in five of 13 nests with prey remains on Tanaga, four of 13 nests on Amchitka, three of 12 nests on Adak, and two of four nests on Amlia.

We collected 191 prey items comprising 19 identifiable

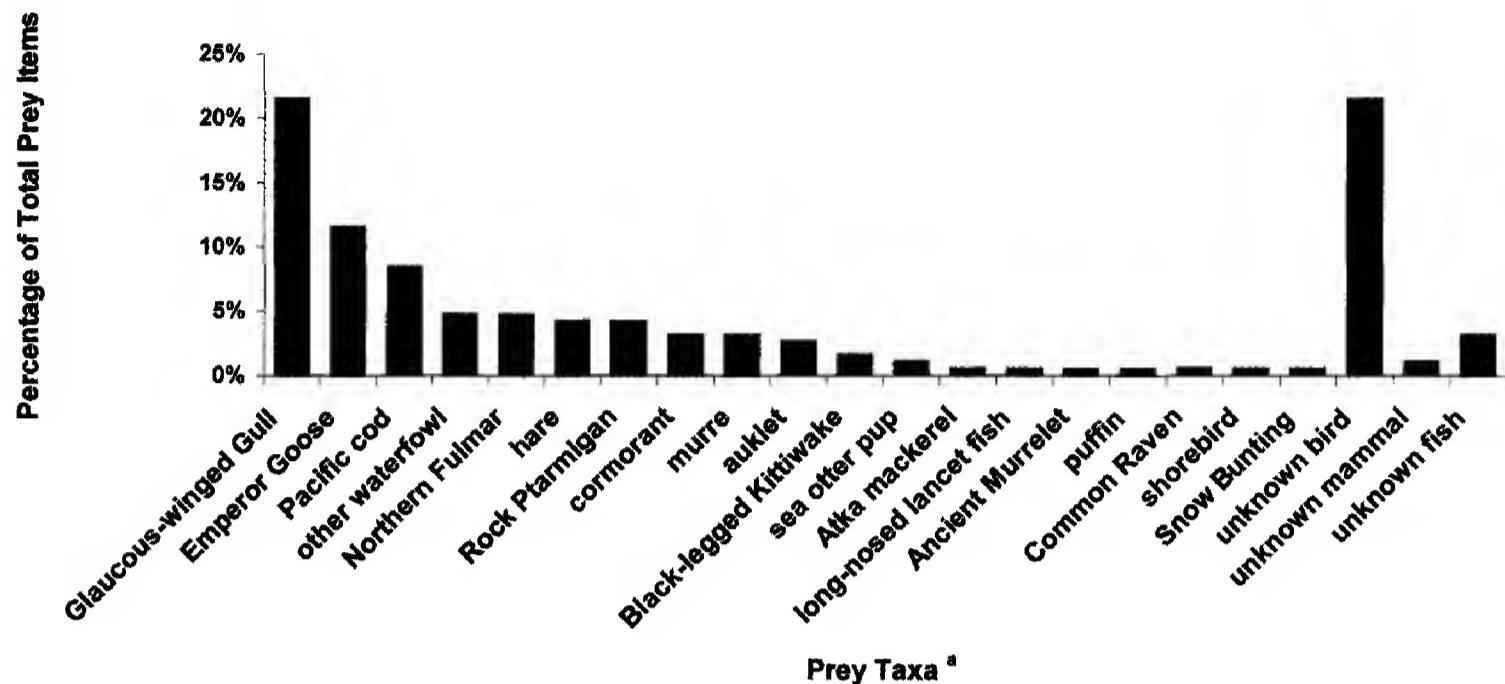


Figure 2. Percent of individual prey items from 191 total prey items found in Bald Eagle nests in the Aleutian Archipelago, April–May 2000–01.^a

^a Scientific names of prey taxa not mentioned in text: Northern Fulmar (*Fulmarus glacialis*), Rock Ptarmigan (*Lagopus mutus*), cormorant (*Phalacrocorax* spp.), murre (*Uria* spp.), auklet: (*Aethia* spp.), Black-legged Kittiwake (*Rissa tridactyla*), Atka mackerel (*Pleurogrammus monopterygius*), long-nosed lancet fish (*Alepisaurus ferox*), Ancient Murrelet (*Synthliboramphus antiquus*), puffin (*Fratercula* spp.), Common Raven (*Corvus corax*), Snow Bunting (*Plectrophenax nivalis*), shorebird (Scolopacidae). Other waterfowl include Mallard (*Anas platyrhynchos*), Northern Pintail (*A. acuta*), Harlequin Duck (*Histrionicus histrionicus*), Red-breasted Merganser (*Mergus serrator*), and unknown waterfowl.

and three unidentifiable prey taxa, indicating that Bald Eagles consumed a variety of prey during our study. However, the distribution of identifiable prey items in eagle diets was skewed towards Glaucous-winged Gulls (*Larus glaucescens*) and Emperor Geese, which composed 21% and 12% of all prey items, respectively (Fig. 2). All other identifiable avian and mammalian prey composed <5% of all prey items. Fish occurred infrequently with the exception of Pacific cod (*Gadus macrocephalus*). Fish and mammalian prey were usually identifiable to species, but 21% of all prey items consisted of unidentifiable avian prey.

DISCUSSION

Emperor Geese remains occurred in Bald Eagle nests and were the second most frequent prey item in Bald Eagle diets. Bald Eagles likely consumed most of these geese at the end of their overwintering period. Our observations provide empirical evidence that Bald Eagles consume Emperor Geese more extensively than previously reported, and help resolve conflicting accounts of Bald Eagle predation on Emperor Geese in the literature. However, the absolute magnitude of eagle predation is unknown because we cannot partition depredated from scavenged Emperor Geese.

Bald Eagle diet breadths are likely constrained throughout winter and early spring because of the absence of anadromous fish and several species of seabirds

such as alcids and procellariiformes available during summer (White et al. 1977, G. Byrd and J. Williams unpubl data). Mammalian prey also are relatively scarce because introduced hares (*Lepus* spp.) occur only in the eastern Aleutians, and sea otters (*Enhydra lutris*) have experienced a 75–88% decline throughout the Aleutians (Doroff et al. 2003). Thus, Emperor Geese may be an important alternative winter food source for Bald Eagles, regardless of how they are acquired (i.e., predation or scavenging). Emperor Geese are available to Bald Eagles because they inhabit protected nearshore reefs and lagoons where eagles forage (Petersen et al. 1994). The harsh Aleutian winter and lack of agricultural foods available to most other species of wintering geese in southern latitudes may weaken Emperor Geese (Schmutz et al 1994), thereby further increasing their vulnerability to predation or eventual scavenging by Bald Eagles. However, we cannot determine the absolute frequency of Emperor Geese in Bald Eagle diets from our data because birds and large bony fish are often over-represented in samples of prey remains collected from eagle nests (Todd et al. 1982, Mersmann et al. 1992), and a high proportion of unknown birds occurred in our sample.

Emperor Geese remains did not occur in Bald Eagle nests searched during 2000. Temporal variation in Bald Eagle nesting chronology likely explains year-year differences. Eagle nesting was delayed apparently in the eastern Aleutians during 2000 because only 26% of eagle

pairs nested by late April–early May (R. Anthony unpubl. data). Spring migration of Emperor Geese usually peaks by mid-April (Eisenhauer and Kirkpatrick 1977), so Emperor Geese likely migrated before eagles began to nest. Conversely, 83% of eagle pairs surveyed in the central and western Aleutians during 2001 nested by late April, thus increasing the probability that depredated or scavenged Emperor Geese would be brought back to eagle nest sites and detected in our searches.

Reported nesting densities of eagles in the Aleutians range from one pair per 7–20 km of coastline (G. Byrd and J. Williams unpubl. data), and we observed over 350 breeding pairs during our surveys (R. Anthony unpubl. data). Assuming that (1) eagle densities are similar during winter which is reasonable given that adults in the Aleutians are likely non-migratory (Murie 1959, White et al. 1971), although sub-adult movements are largely unknown; (2) our results are representative of consumption of Emperor Geese by Bald Eagles during the entire overwintering period for Emperor Geese; and (3) at least some proportion of geese are depredated rather than scavenged, Bald Eagles may contribute more to Emperor Goose mortality than previously thought.

RESUMEN.—Las causas de mortalidad del ganso emperador migratorio (*Chen canagica*) una especie de manejo especial en Alaska, se conocen pobremente. Evaluamos la relativa frecuencia del consumo por parte del águila calva (*Haliaeetus leucocephalus*) de gansos emperadores a lo largo de las islas del archipiélago Aleutiano, identificando restos de presas de 94 nidos de águilas calvas durante Abril–Mayo, 2000–01. Encontramos partes no identificables de gansos emperador en el nido de águilas calvas con restos de presas ($N = 18$) durante 2000. Inversamente, 39% de los nidos con restos de presas ($N = 57$) contenían gansos emperador durante 2001. El ganso emperador constituyó 12% de todos los ítem presa individuales encontrados en los nidos de águila calva durante 2000–01. Aunque nuestros métodos no pueden distinguir depredación de alimentación por carroña y los restos de presa fueron evaluados al final del periodo de sobre invernación del Ganso emperador, las águilas calvas pueden ser una fuente significativa de mortalidad para el ganso emperador durante el invierno en las islas Aleutianas. Además, el ganso emperador puede ser un componente importante de la dieta para las águilas calvas que pasan el invierno en los mismos territorios donde se reprodujeron.

[Traducción de César Márquez]

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SURVIVAL AND BEHAVIOR OF A ONE-FOOTED MADAGASCAR FISH-EAGLE IN THE WILD

RUTH E. TINGAY¹ AND MICHÉLE L. CLARKE

School of Geography, University of Nottingham, Nottingham, NG7 2RD U.K.

RICHARD T. WATSON AND RUSSELL THORSTROM

The Peregrine Fund, 5668 Flying Hawk Lane, Boise, ID 83709 U.S.A.

LOUKMAN KALAVAH

The Peregrine Fund, P.O. Box 4113, Antananarivo 101 Madagascar

KEY WORDS: *Madagascar Fish-Eagle; Haliaeetus vociferoides; amputation; dominance hierarchy; longevity.*

The ability of a one-footed raptor to survive long-term in the wild has been considered questionable (Cooper et al. 1980, Durham 1981). While there are accounts of the survival of one-legged raptors in captivity (Cooper 1985) and of those admitted from the wild to a raptor clinic (Durham 1981), we could only locate two published accounts detailing the known survival of one-footed raptors in the wild. Blodget et al. (1990) document the 2-yr survival in the wild of a one-footed immature Bald Eagle (*Haliaeetus leucocephalus*) and Eggenhuizen (1995) documents the 1-mo survival in the wild of a one-legged adult Eurasian Kestrel (*Falco tinnunculus*), killed ultimately by impact with a vehicle. Avian anatomical constraints (McKeever 1979, Cooper 1985) and species-specific foraging strategies (Cooper et al. 1980) suggest that one-footed raptors have a diminished capacity for long-term survival in the wild. Here, we report the 7-yr survival, in the wild, of a one-footed adult male Madagascar Fish-Eagle (*Haliaeetus vociferoides*) and document his behavior and social status within a polyandrous breeding trio.

STUDY AREA AND METHODS

The Peregrine Fund initiated the Madagascar Fish-Eagle Conservation Program on Madagascar's western seaboard in 1991, to study the species' ecology and breeding behavior (Watson et al. 1993). Through 2001, over 100 Madagascar Fish-Eagles were trapped and banded with a uniquely numbered embossed aluminum band and a series of colored plastic or colored aluminum bands for individual identification. The majority of fish-eagles were trapped at lakes in the Manambolomaty River floodplain (19°00'S, 44°30'E) in the Antsalova region of western Madagascar, ca. 300 km west of the capital, Antananarivo. The habitat is dominated by tropical, deciduous, dry forest containing several lakes (with areas of 3.1–4.9 km²) that support 11 fish-eagle territories (Rabarisoa et al. 1997).

On 8 November 1996, a one-footed adult male Madagascar Fish-Eagle was trapped in a territory on Lake Befotaka known as "Befotaka 2." The eagle's right foot was missing, severed at the distal tip of the tarsometatarsus, which had healed over to form a flat-based stump measuring 30 mm × 27 mm. There were no signs of infection and we evaluated the eagle as being in otherwise good condition. An aluminum band (0118) was fitted to the left leg and the eagle was released. A one-footed adult male fish-eagle with an aluminum band on its left leg was resident in the Befotaka 2 territory throughout 1997 and 1998 and was assumed to be the same bird (Kalavah 1997, 1998).

During the 1999–2001 breeding seasons (May–Septem-

¹ E-mail address: dimlylit100@hotmail.com

ber), daily behavioral observations were made of marked fish-eagles at lakes on the Manambolomaty River floodplain, to document the social interactions of polyandrous breeding trios and quartets (Tingay 2000). Observations were made from land or boat from distances ranging from 5–500 m using 8 × 32 and 10 × 42 binoculars and a 25–60× zoom telescope. Fish-eagles were trapped using either a noosed fish (Wiersma et al. 2001) or a noose carpet (Bloom 1987) and blood samples were taken to conduct DNA studies on paternity and intra-population relatedness (Tingay et al. 2002). Fish-Eagle 0118 was included in this study as he was a member of a breeding trio located within the Befotaka 2 territory.

RESULTS

Survival Longevity. On 18 August 1999, the continued presence of eagle 0118 in Befotaka 2 territory was confirmed when he was re-trapped using a noosed fish and positively identified by the aluminum leg band number. He was re-trapped twice more on 20 August 1999 on both a noose carpet and a noosed fish trap, placed for the second resident adult male fish-eagle from this territory (0008). A one-legged fish-eagle, banded on the left leg and observed in the Befotaka 2 territory during 2000 was assumed to be bird 0118. He was last re-trapped in the Befotaka 2 territory on 4 August 2001 with a noosed fish. A resident one-legged eagle banded on the left leg and present in Befotaka 2 at the time of writing (May 2003) was also assumed to be bird 0118.

Observed Behavior. Fish-eagle 0118 was observed foraging, and involved with courtship and breeding activities. He snatched fish from the lake surface with his left foot and carried it to perch in a tree. He used his left foot to hold the fish in place and used the stump of his right leg to balance, enabling him to lean forward and tear the fish with his beak. Fish-eagle 0118 participated fully in courtship and nesting activities, which included copulation, nest building, incubation and brooding, prey delivery, and nest defense. During copulation, he appeared to use his stump and out-stretched wings to aid his balance, while on the female's back. To facilitate nest building, Madagascar Fish-Eagles fly close to a tree and use both feet to snap off twigs and greenery and deliver them to the nest. Fish-eagle 0118 was observed collecting twigs and greenery successfully in the same manner using only his left foot. This eagle also defended the nest and its immediate vicinity from potential predators such as Yellow-billed Kite (*Milvus aegyptius*; Sinclair and Langrand 1998), Madagascar Buzzard (*Buteo brachypterus*), and Pied Crow (*Corvus albus*), by engaging in aerial pursuits and loud vocalizations with his conspecifics.

Social Status. Fish-eagle 0118 was presumed to be the dominant male in the Befotaka 2 territory, based on his level of paternal investment at the nest and his level of aggression towards the other male (0008) in the territory (Tingay 2000). During each observation period he was aggressive towards eagle 0008, typically supplanting 0008 from either the nest or perches near it. Supplanting was

achieved either by flying towards eagle 0008 and emitting the distinctive "displacement call" (Tingay 2000), resulting in 0008 leaving his position before eagle 0118 arrived. Alternatively, eagle 0118 landed next to bird 0008 and physically moved 0008 by pushing body against body. On several occasions, eagle 0118 was also observed foot grappling with 0008, typically when eagle 0008 attempted to deliver a stick or greenery to the nest. On these occasions eagle 0118 flew towards 0008, making the displacement call, and attempted to intercept bird 0008's flight to the nest. When eagle 0008 continued towards the nest, bird 0118 pushed out his left foot and 'locked' with one of 0008's feet for several seconds before both released their grip and they separated. Fish-eagle 0118 successfully removed or supplanted 0008 during every observed aggressive act throughout the three breeding seasons (1999–2001).

DISCUSSION

There are several possible explanations to account for the loss of fish-eagle 0118's right foot. He may have become accidentally entangled in a fisherman's net while foraging and had his foot cut off to release him (Rabarisoa et al. 1997). It is possible that eagle 0118 was used to supply eagle body parts to a traditional sorcerer who believed that the addition of an eagle foot or beak to a potion would give it strengthened properties (Kalavah and Razanrizanakanirina 1997). An alternative explanation may be that his foot was removed by locals to obtain a leg band; aluminum leg bands had been mistaken as silver or another precious metal (Kalavah and Razanrizanakanirina 1997). Another possible explanation is that eagle 0118 was the victim of a Nile crocodile (*Crocodylus niloticus*) attack while bathing or drinking at the lake edge, similar to the crocodile attack on an Osprey (*Pandion haliaetus*) reported from West Africa (Hutton 2001).

It has been argued that birds have a limited amount of soft tissue in the distal portion of the leg and a reduced vascular supply to the extremities (Proctor et al. 1993), rendering them with a limited ability to fight foot infection (Durham 1981, Cooper 1985). In addition, the proper distribution of a bird's weight requires the use of both feet; otherwise the additional weight borne by one foot could lead to the deterioration (and thus infection) of the epithelium of the toe pad (McKeever 1979, Durham 1981, Cooper 1985). We suggest that fish-eagle 0118 has used his stump to aid his balance and thus his weight distribution, and may have reduced his susceptibility to these kinds of problems and increased his survival longevity.

Another consideration that may affect the ability of a one-footed raptor to survive in the wild is the bird's ability to forage effectively. Cooper et al. (1980) and Durham (1981) suggest that foot loss may be more of a problem for specialized rapacious species such as Accipiters, but less of a problem for generalist predators such as Buteos. The Madagascar Fish-Eagle is a specialized piscivorous

raptor (Berkelman et al. 1999), yet there is no evidence to suggest that 0118's handicap affected his foraging ability.

Belonging to a breeding trio may have been advantageous for eagle 0118 and could have contributed to his longevity, although other two-footed Madagascar Fish-Eagles also engaged in this breeding strategy (Tingay et al. 2002). Fish-eagle 0118's dominant social status was surprising, as a handicapped eagle may have been expected to be bullied by both conspecifics and other species (Blodget et al. 1990). The fact that eagle 0118 dominated another group member, 0008, suggests that he was not intimidated by conspecifics. Additionally, fish-eagle 0118 was not intimidated by other species, as demonstrated by his frequent involvement in nest defense against potential predators.

Age may also have influenced the dominance hierarchy in this territory. The exact age of eagle 0118 was unknown, although he was in adult plumage when trapped in 1996 and therefore at least 4 or 5 yr old at time of capture, making him at least 11–12 yr old at the time of writing. Fish-eagle 0008 was known to be younger than eagle 0118, as banding records showed he hatched in a neighboring territory in 1993.

While we are not advocating the general release of one-legged raptors to the wild, fish-eagle 0118 may illustrate an important exception to the rule. The Madagascar Fish-Eagle is considered critically endangered (Collar et al. 1994) with a census population currently estimated at 222 individuals (Rabarisoa et al. 1997). The effective population size of any species is usually smaller than the census population size (Lande and Barrowclough 1993) and thus every potential breeding fish-eagle adult is important to the overall genetic diversity of the species. Fish-eagle 0118 is known to possess at least one rare allele shared with only one other eagle in the area (Tingay et al. 2002) making him a potentially critical genetic contributor. His 7-yr survival in the wild as well as holding a socially dominant position in the group demonstrates his ability to adapt, and provides an alternative management option to the capture and retention in captivity of disabled individuals of endangered species.

RESUMEN.—Reportamos la supervivencia por 7 años en vida silvestre de un águila-pescadora de Madagascar con una sola pata y documentamos su estatus social como macho dominante dentro de un trío poliandrico. Esta águila pescadora fue observada forrajeando exitosamente y participando en actividades reproductivas tales como copulación, construcción del nido, incubación, empollamiento, entrega de presas y defensa del nido.

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REPRODUCTIVE SUCCESS OF SPOTTED OWLS SYMPATRIC WITH BARRED OWLS IN WESTERN WASHINGTON

WAYNE F. IVERSON¹

Science Department, Newport High School, 4333 Factoria Blvd. SE, Bellevue, WA 98006 U.S.A.

KEY WORDS: *Northern Spotted Owl*; *Strix occidentalis caurina*; *northern Barred Owl*; *Strix varia varia*; *competition*; *Washington*.

Northern Barred Owls (*Strix varia varia*) and northern Spotted Owls (*Strix occidentalis caurina*) in western Washington use similar forested habitats (Herter and Hicks 2000) and demonstrate some niche overlap in their predation upon small mammals (Hamer et al. 2001). Both owls also use similar tree cavities for nesting (Hamer 1988). Because Barred Owls are larger (Dunning 1992) and exhibit more pronounced territorial behavior (Hamer et al. 2001), many biologists have expressed concern that Barred Owls may pose a significant obstacle to the successful recovery of the threatened northern Spotted Owl. Kelly et al. (2003) found that Spotted Owl site occupancy was negatively affected by close proximity to Barred Owls in forests on the eastern slope of the Washington Cascades and on the Olympic Peninsula. Recently, Pearson and Livezey (2003) observed that the loss of mature forest habitat may reduce the survivability of Spotted Owls in the presence of Barred Owls. My study examined potential effects of Barred Owls on Spotted Owl reproductive success on the western slope of the Washington Cascades.

STUDY AREA AND METHODS

Located on the western slope of the Washington Cascades (ca. 47°–49°N, 121°–122°W), the Mount Baker-Snoqualmie National Forest (MBSNF) is ideally suited to evaluate effects of interactions between Spotted and Barred owls. The two species have co-occurred in this area for over 20 yr (Taylor and Forsman 1976). Spotted Owls in the MBSNF are near the northern limit of their range and are less productive than owls in warmer or drier parts of their range (Iverson 1996). Therefore, Spotted Owls in the MBSNF might be expected to be more vulnerable to potential exclusion by more aggressive Barred Owls.

Reproductive success is an important component of individual fitness. For the purposes of this study, I defined reproductive success as the production of young in one or more survey years. If competition (or predation) by Barred Owls were a significant threat to Spotted Owls, one would expect to see reduced reproductive success of Spotted Owl activity centers that are coincident with Barred Owls. Spotted Owl activity centers in this study were determined by a hierarchical system, with a nest site being the most reliable definition, followed by owls with young, consistent daytime location, and consistent nighttime location (U.S. Forest Service 1988). Using the mean annual home range estimate for Spotted Owls (3-km radius circle) and Barred Owls (1.5-km radius circle) in this area (Hamer 1988), it is very likely that Barred Owls found consistently within 2.5 km of Spotted Owl activity centers have home ranges that overlap those of Spotted

¹ E-mail address: iversonw@bsd405.org

Table 1. Spotted Owl activity-center occupancy, composition of older forest, and presence of Barred Owls: the presence of Barred Owls in Western Washington. BO++ = Barred Owl within 0.8 km, BO+ = Barred Owl within 2.5 km, BO- = Barred Owl not within 2.5 km. Site occupancy codes: S = single owl, PR = pair confirmed, PN = nesting pair, PF = pair with fledglings (number of owlets), 0 = unoccupied.

SPOTTED OWL SITES	BARRED OWLS	STATUS 1990	1991	1992	ELEVATION (M)	OLDER FOREST (%)
121	BO+	PF (1)	PF (1)	PN	837	46.0
122	BO+	S	S	O	713	63.3
171	BO+	S	S	S	543	53.0
173	BO++	O	PF (1)	PN	744	53.8
192	BO+	S	S	S	992	—
202	BO++	O	O	O	744	50.4
217	BO+	PF (1)	O	PF (1)	1116	56.8
231	BO-	PR	PR	S	1054	40.3
267	BO+	S	PR	PF (1)	651	32.3
268	BO-	S	PR	S	868	20.7
269	BO-	S	S	S	868	41.5
514	BO++	S	PF (2)	PN	930	—
526	BO++	S	PR	PF (1)	930	—
631	BO-	PF (1)	S	PN	434	68.2
638	BO-	S	PR	PR	521	25.0
710	BO+	S	S	S	775	51.1
719	BO-	PN	PF (1)	PF (2)	992	24.8
727	BO+	S	S	PF (2)	977	36.2
731	BO+	S	S	PF (2)	806	34.9

Owls (T. Hamer pers. comm.). Based on this assumption, I compared reproductive success of Spotted Owl pairs with and without Barred Owls.

I surveyed 19 Spotted Owl activity centers in the MBSNF according to standard protocol (U.S. Forest Service 1988) for three consecutive years (1990–92). Surveys were conducted during the breeding season (15 March–31 August) using a vocal imitation or tape recording of Spotted Owl calls. Spotted Owl activity centers were surveyed at least three times in each year to determine status (unoccupied, single owl, or owl pair with or without fledglings). Barred Owls respond to Spotted Owl calls and were inventoried simultaneously (Dunbar et al. 1991). I did not make an effort to determine Barred Owl activity-center status, however.

The activity center was considered to be the center of a Spotted Owl home range. I used the MBSNF geographic information system to estimate the percent cover of older forest (trees >53 cm Diameter Breast Height) available to owls at each site within a 3-km radius of the activity center. The 3-km radius gives a good approximation of habitat available in Spotted Owl annual home ranges (Lehmkuhl and Raphael 1993). There was no timber harvesting (or other management activity) within 3 km of the activity centers during the years in which I surveyed them.

I used a contingency analysis and *G*-test (Zar 1984) to evaluate the effect of Barred Owl presence or absence on Spotted Owl reproductive success. Mann-Whitney *U*-tests (Zar 1984) were used to evaluate differences between

means. All means are expressed \pm SE. Alpha levels of all statistical tests were set at 0.05.

RESULTS AND DISCUSSION

Of the 19 Spotted Owl activity centers in this study, 13 had Barred Owls within 2.5 km (BO+) and six did not (BO-). Of the 13 BO+ activity centers, 8 (62%) fledged young successfully in at least one of the 3 yr, while only two (33%) of BO- activity centers were successful (Table 1). Spotted Owl reproductive success was independent of Barred Owl presence or absence (Contingency analysis, $G = 1.326$, $P = 0.25$).

The amount of older forest available to Spotted Owls varied substantially across all sites (range = 20.7–68.2%). The mean amount of older forest available at BO+ sites was $47.8 \pm 3.2\%$ and $36.8 \pm 7.2\%$ at BO- sites. There was no significant difference in amount of available older forest habitat between BO+ and BO- sites (Mann-Whitney test, $U_{0.05(2),6,10} = 49$, $U = 16$, $U' = 44$). Sixteen of the 19 activity centers were in the Pacific silver fir (*Abies amabilis*) elevation zone (Franklin and Dyrness 1973), while only three were in the lower elevation western hemlock (*Tsuga heterophylla*) zone. BO+ activity centers were at a mean elevation of 828 ± 43.6 m. The mean elevation of BO- activity centers (790 ± 103.6 m) was not significantly different (Mann-Whitney test, $U_{0.05(2),6,13} = 62$, $U = 39.5$, $U' = 38.5$).

Kelly et al. (2003) found a significant effect on Spotted Owl site occupancy when Barred Owls were within 0.8 km, but they did not report on the reproductive success of Spotted Owls. My *post-hoc* analysis of MBSNF Spotted Owl activity centers that had Barred Owls within 0.8 km (Table 1) revealed that three of the four sites were reproductively successful, averaging 1.3 ± 0.3 fledglings per site during the study period. Five of the remaining 9 BO+ activity centers were reproductively successful, averaging 1.8 ± 0.2 young per site. The two reproductive BO- sites averaged 2.0 ± 1.0 fledglings. There could be some effect of Barred Owls indicated by the inverse relationship between Barred Owl proximity and mean fledglings produced per site. But there were also an equal number of total owlets fledged comparing BO++ (Barred Owls within 0.8 km) and BO- sites.

Habitat qualities (other than amount of older forest) may account for some of the differences between my study and others. For example, Spotted Owl activity centers in Olympic National Park (S. Gremel pers. comm.) are more productive in the Pacific silver fir zone than activity centers in lower elevation forests. Similarly, most of the productive MBSNF Spotted Owl activity centers were found in the Pacific silver fir zone.

Niche differences may also help explain the success of Spotted Owls (BO+) in the MBSNF compared to other areas. The diet of Spotted Owls on the western slope of the Washington Cascades includes fewer flying squirrels (*Glaucomys sabrinus*) and more deer mice (*Peromyscus maniculatus*) and pikas (*Ochotona princeps*) than the diets of Spotted Owls in the Olympics and the eastern slope of the Washington Cascades (Forsman et al. 2001). Mean prey mass is also smaller for MBSNF owls than owls in the other two locations (Forsman et al. 2001).

Hamer et al. (2001) noted significant differences in foraging by Barred Owls and Spotted Owls in the MBSNF, with Barred Owls taking more diurnal animals and prey associated with wetter habitats. Spotted Owls also consume more arboreal and semi-arboreal mammals than Barred Owls (Forsman et al. 2001, Hamer et al. 2001), which may be related to the larger foot spread of Spotted Owls (Hamer 1988).

According to Mayr and Short (1970), Barred and Spotted owls diverged as separate species relatively recently. The exact origin of the two species is not known, but the modern range expansion of Barred Owls into the Pacific Northwest is not the first time these species have been sympatric. The historical ranges of Barred Owls and Spotted Owls overlap in Mexico's Sierra Madre Occidental (Johnsgard 2002), where they occupy the same forest types and elevation zones (Enríquez-Rocha et al. 1993). There are apparently significant enough niche and habitat differences to allow Barred Owls and Spotted Owls to coexist in at least some areas.

RESUMEN.—Diecinueve centros de actividad del Búho moteado en el Bosque Nacional Monte Baker-Snoqual-

mie fueron estudiados por tres años consecutivos (1990–92). La presencia de los Búhos barreteados fue determinada simultáneamente debido a que los búhos barreteados responden a los llamados del búho moteado usados durante los estudios. Trece de los centros de actividad de los búhos moteados tenían búhos barreteados dentro de 2.5 km y seis no. Sesenta y dos por ciento de los centros de actividad del búho moteado con búhos barreteados produjeron volantones en al menos uno de los tres años, pero únicamente 33% de los centros de actividad sin búhos barreteados tuvieron éxito reproductivo.

[Traducción de César Márquez]

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HISTORICAL AND CURRENT STATUS OF BREEDING AND WINTERING WESTERN BURROWING OWLS (*ATHENE CUNICULARIA HYPUGAEA*) IN TEXAS

NANCY E. MCINTYRE¹

Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409-3131 U.S.A.

KEY WORDS: *Western Burrowing Owl*; *Athene cunicularia hypugaea*; *abundance*; *Breeding Bird Atlas*; *Breeding Bird Survey*; *Christmas Bird Count*; *population trend*; *Texas*.

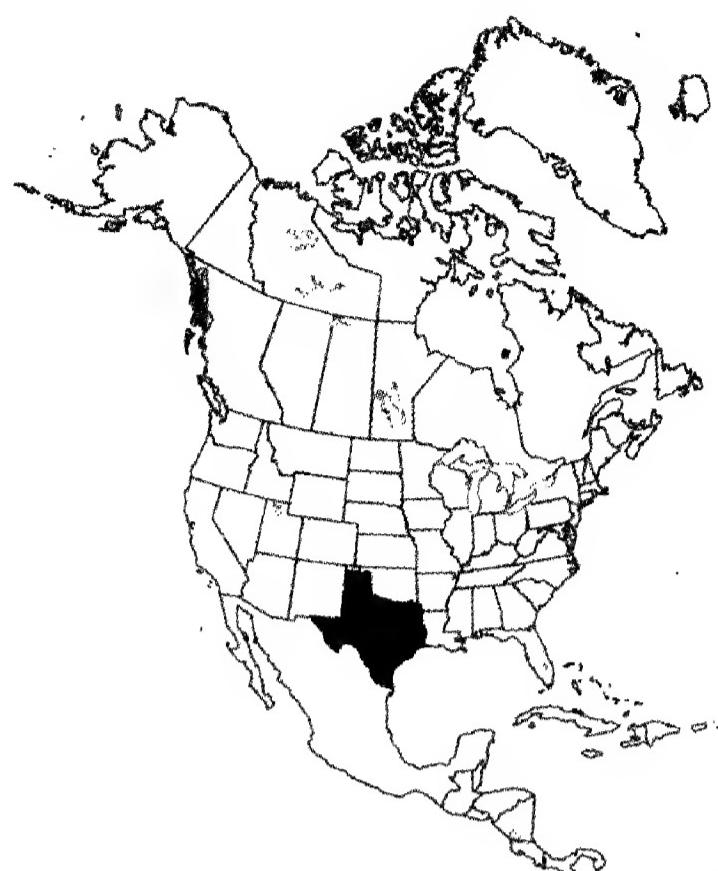
The western Burrowing Owl (*Athene cunicularia hypugaea*) is one of 18 New World Burrowing Owl subspecies, and one of only two in North America. Designated Endangered in Canada and Threatened in Mexico, the Burrowing Owl is a U.S. Fish and Wildlife Service (USFWS 2001) Bird of Conservation Concern in Regions 1 (Pacific), 2 (Southwest), and 6 (Mountain-Prairie). It is state-listed as Threatened in Colorado, Endangered in Iowa and Minnesota, and has been additionally listed in 16 other U.S. states (Arizona, California, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, Oregon, South Dakota, Texas, Utah, Washington, and Wyoming) as a species of special concern (James and Espie 1997, Sheffield 1997, USFWS 2001). Population declines and range contractions have been noted at various locations throughout North America, prompting calls for more information about the species' historic and current population status that may be used to guide conservation efforts (Holroyd et al. 2001). Such assessments have been done for owl populations in sev-

eral U.S. states (e.g., Brown 2001, Korfanta et al. 2001, Martell et al. 2001, Murphy et al. 2001), Canada (Kirk and Hyslop 1998, Shyry et al. 2001), Mexico (Enriquez-Rocha et al. 1993), and North America as a whole (James and Ethier 1989), and they have documented declines in both breeding and wintering owl numbers.

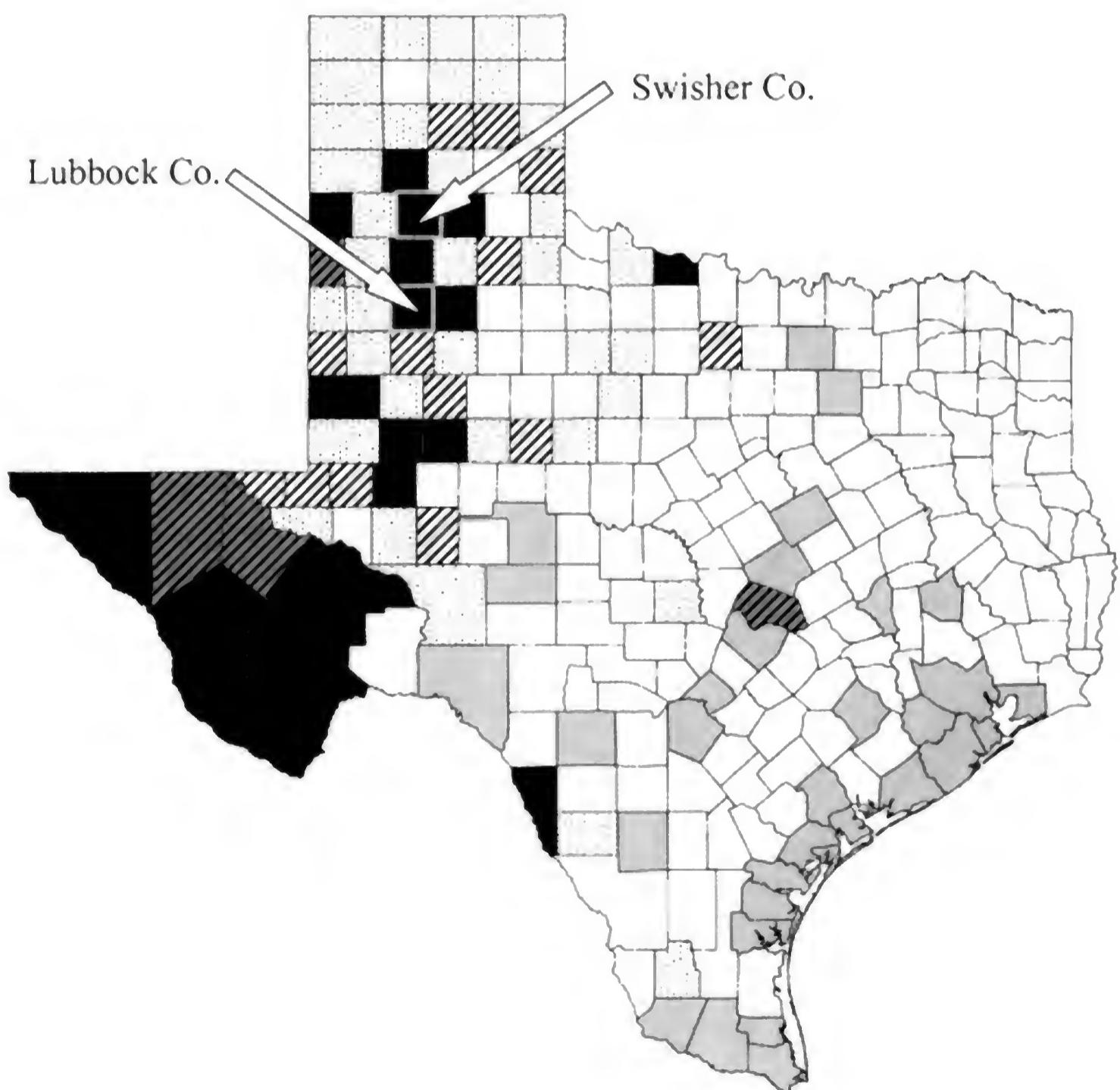
One state that has not had an assessment of its Burrowing Owl population, however, is Texas. Importantly, Texas consistently accounts for a substantial portion of the overall North American owl population in the Breeding Bird Survey, Christmas Bird Counts, and in a recent wildlife agency survey (James and Espie 1997). Indeed, the highest reported relative abundances of overwintering owls come from Texas (USGS 2003), and Texas also supports a sizeable population during the breeding season (James and Espie 1997).

This oversight in the knowledge base was recently recognized, and an explicit call for research on the abundance of western Burrowing Owls in Texas was made (Wellicome and Holroyd 2001). In-depth studies on the coastal population are underway involving the USFWS, Canadian Wildlife Service, and Texas Parks & Wildlife (<http://www.cerc.usgs.gov/frs-webs/gulf-coast/owl.htm>). Given that declines in owl populations in the adjacent states of New Mexico and Oklahoma have been documented (Arrowood et al. 2001, Sheffield and Howery 2001) and that the owl has reportedly suffered from

¹ E-mail address: nancy.mcintyre@ttu.edu



- [Dotted pattern] Breeding
- [Cross-hatched pattern] Hypothetical Breeding
- [Light gray] Winter
- [Solid black] Year-round
- [White box] No Owls Recorded



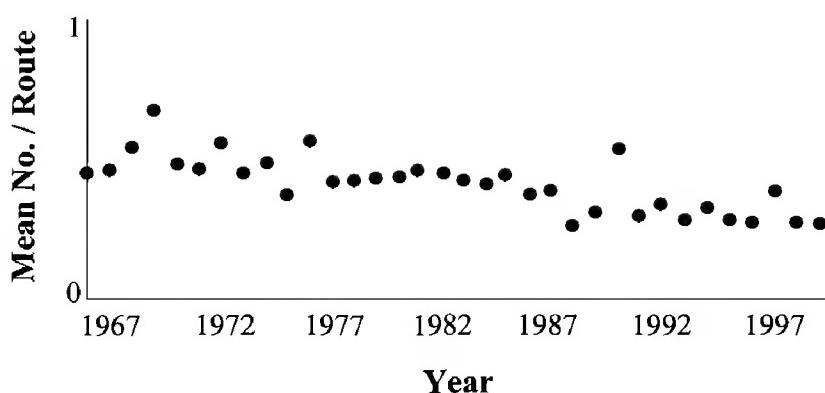


Figure 2. Plot of the mean number of western Burrowing Owls per Breeding Bird Survey route for the state of Texas, by year (1966–99).

range contractions in parts of North America (Wellicome and Holroyd 2001), information about the status of the western Burrowing Owl in Texas would fill a crucial gap in our knowledge. Therefore, in this paper I provide an assessment of western Burrowing Owl abundance in Texas for both the breeding and winter seasons, using historic records (back to 1960) up to current information (2001), and note whether any changes in owl abundance have occurred over that time. In so doing, I provide a current distribution map for the counties of Texas for both breeding and wintering periods. My analysis illustrates that gaps still exist in our knowledge of the western Burrowing Owl.

METHODS

A variety of techniques has been used to assess the status of the western Burrowing Owl, including questionnaires (e.g., Arrowood et al. 2001, Brown 2001), call-playback studies (Shyry et al. 2001), examinations of museum collection records (Enriquez-Rocha et al. 1993), resurveying areas where owls were historically recorded (e.g., Murphy et al. 2001, Korfanta et al. 2001), and summaries of long-term population survey data. I used data from the USFWS's annual Breeding Bird Survey (BBS; 1966–99) and from the Texas Breeding Bird Atlas, which represents a compilation of records from 1987–92 (Benson and Arnold 2001) to document owl abundance during the breeding season. I used data from the National Audubon Society's annual Christmas Bird Count (CBC; 1960–2001) to obtain information about owl abundance during the winter. Although the CBC has been conducted since 1900 in Texas, surveys were intermittent until 1909, and few surveys were conducted in the western por-

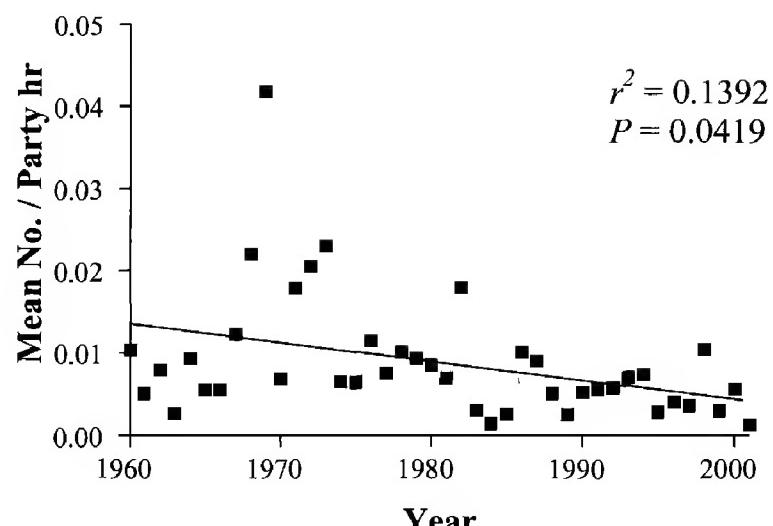


Figure 3. Plot of the mean number of western Burrowing Owls per party-hour per Christmas Bird Count circle for the state of Texas, by year (1960–2001). The slope of the regression line is significantly different than 0 ($r^2 = 0.1392$, $P = 0.0419$).

tion of the state until the 1930s, making consistent information about Burrowing Owls unavailable until 1936. Because survey protocols and circle sizes were not standardized until the late 1950s, however, data prior to 1960 are excluded from analysis. Other researchers have similarly used either BBS (Arrowood et al. 2001) or both BBS and CBC (Kirk and Hyslop 1998, Sheffield and Howery 2001) data to document historic and current western Burrowing Owl population trends.

The BBS data represented the mean number of owls recorded per route for each year; the CBC data represented the mean number of owls recorded per plot circle for each year. Only those routes and circles that reported the presence of western Burrowing Owls were included in analyses (i.e., data were not averaged over all routes/circles in the state). CBC data were also standardized by party-hour each year. Mean abundance data were plotted by year, and linear regression analysis was used to detect any significant trends in owl abundance over time.

BBS route information, CBC records, and information from the Texas Breeding Bird Atlas were used to construct a distributional map for the western Burrowing Owl in Texas, by county (Fig. 1). Additional data for Swisher County (indicated on Fig. 1) came from Ross and Smith (1970).

RESULTS

An examination of the distributional county map (Fig. 1) shows that many gaps still exist in our knowledge of



Figure 1. Distributional map for the western Burrowing Owl in Texas, by county. If at least one breeding or overwintering occurrence was recorded in a county, the county is shaded (stippled for breeding record only, gray for winter record only). If a county had both breeding and overwintering records, it is shaded black. Unshaded counties had no records of western Burrowing Owls. The "hypothetical breeding" (striped) category includes both "Possible" and "Probable" localities from the Texas Breeding Bird Atlas that were not confirmed otherwise by BBS data. Note that the hypothetical breeding category can co-occur with winter records (gray stripes). Lubbock and Swisher counties (mentioned in text) are indicated.

the spatial and temporal distribution of western Burrowing Owls in Texas. These gaps may be explained in part by a lack of Breeding Bird Survey routes and Christmas Bird Count circles in many parts of Texas. Because of this patchy distribution of survey sites, there are numerous counties where owls likely occur, but have never been recorded in certain seasons or at all; our knowledge about the distribution of the western Burrowing Owl would benefit greatly from a survey of these likely counties. In addition, the number of owls that winter in Texas may be underestimated if CBC surveys are conducted during inclement weather when the owls are most likely to be in their burrows and not in view (Butts 1973).

No significant changes were found in the mean number of western Burrowing Owls during the breeding season from 1966–99 ($P = 0.2498$; Fig. 2). The slope was negative (-2.04), suggesting a population decline, but this trend was not significantly different from zero over the past 34 yr. However, the mean number of owls recorded has been consistently low (Fig. 2).

A significant decline was detected in the mean number of overwintering owls from 1960–2001 ($r^2 = 0.1392$, $P = 0.0419$; Fig. 3); there have not been any large peaks in mean owls recorded since the early 1970s. Lubbock County has consistently reported the highest numbers of owls in winter (averaging 3–10 owls per circle), especially in recent years (recorded highest owl counts in 8 of the past 15 yr and always among the 10 highest counts in the state during the past 15 yr; USGS 2003).

DISCUSSION

There are limitations in using BBS and CBC data that pertain to differences in participant effort and skills (Sauer et al. 1994, Peterson 1995) and the lack of consensus about which statistical method for estimating population trends is the most appropriate (Thomas 1996), and caution has been urged when using trend data to recommend conservation actions (Dunn 2002). Despite these shortcomings, the value of such long-term data is acknowledged (James et al. 1996). The trends noted in the present study should therefore be placed in the larger context of similar evaluations that have been conducted for western Burrowing Owls in other U.S. states, Canadian provinces, and Mexican states (e.g., Enriquez-Rocha et al. 1993, Kirk and Hyslop 1998, Shry et al. 2001, Vercauteren et al. 2001). This study thus complements previous work and fills a gap in our knowledge about the overall population trajectory of the western Burrowing Owl.

No significant changes were found in the mean number of western Burrowing Owls during the breeding season from 1966–99, although the trend was downward. An earlier, shorter-term analysis of BBS data revealed a similar suggestive, but statistically non-significant, decline (Sheffield 1997). Significant declines in the number of breeding owls over limited periods of time have been reported from the Panhandle and Trans-Pecos regions of Texas (Haug et al. 1993), however, suggesting that local-

ized populations may not conform to the overall state pattern. The statistically significant decline in overwintering owls (particularly since the 1970s) mirrors a pattern seen in California (Sheffield 1997).

Texas is fortunate to support both breeding and overwintering populations of the western Burrowing Owl as well as both resident and migratory populations (Ross and Smith 1970, Butts 1973). Indeed, Texas has been considered a “promising location for future studies” on the species (Wellcome and Holroyd 2001). Owl numbers are low, however, and thus merit concern. In addition, the number of wintering owls has declined over the past few decades. Because the western Burrowing Owl is a conservation priority by the USFWS as well as by various state and provincial agencies, information about the abundance and distribution of the owl is important for determining current and future management actions and goals. A continuation of monitoring studies such as BBS and CBC is clearly needed, along with much more research on the western Burrowing Owl in Texas and elsewhere (Wellcome and Holroyd 2001). An expansion of the coverage currently provided by the BBS and CBC would supplement our knowledge of how abundant the species is in portions of the state that are currently unsampled.

Because Texas represents the area of highest abundance of overwintering western Burrowing Owls in the US (USGS 2003), the decline in winter owl abundance possibly reflects reduced numbers observing owl populations elsewhere in North America. Banding studies would help resolve this issue by identifying whether owls that overwinter in Texas are from declining breeding populations from Canada. Identifying the cause(s) behind the decline in overwintering birds is necessary if this decline is to be halted and reversed, but potential causes of the decline will remain undetermined unless more in-depth studies are completed.

RESUMEN.—Una compilación de los datos sobre las poblaciones reproductivas y sobre invernantes del búho cavador oriental (*Athene cunicularia hypugaea*) del Estudio de Reproducción de Aves (1966–99), los conteos Nacionales de Aves (1960–2001), y del Atlas de Reproducción de Aves de Texas (1987–92), revelaron que mientras la abundancia de búhos en la estación reproductiva permaneció relativamente baja pero constante en unas cuantas de las décadas pasadas, el número de búhos en el invierno ha decaído. Debido a que Texas representa el área con la más alta abundancia de búhos cavadores occidentales sobre invernantes, este declive posiblemente está reflejando el decrecimiento en las poblaciones reproductivas de búhos notada en otros sitios de Norteamérica. Un mapa de la distribución en Texas por condado, de los búhos durante su reproducción y durante la temporada invernal, fue compilado y reveló que aún existían algunos vacíos en nuestro conocimiento sobre donde están los búhos en Texas. Esta información prob-

ablemente será útil para guiar los planes de manejo invernal y para estimular mayor investigación sobre el búho cavador occidental en Texas y en cualquier otra parte de su rango.

[Traducción de César Márquez]

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SERUM CHEMISTRY VALUES FOR NESTLING BALD EAGLES (*HALIAEETUS LEUCOCEPHALUS*) IN FLORIDA BAY, EVERGLADES NATIONAL PARK

BRIAN MEALEY,¹ GRETA M. PARKS, CARLOS M. PAGES

Falcon Bachelor Bird of Prey Center, Miami Museum of Science, 3280 South Miami Avenue, Miami, FL 33129 U.S.A.

BRIAN A. MILLSAP²

*Bureau of Wildlife Diversity Conservation, Florida Fish and Wildlife Conservation Commission,
 620 South Meridian Street, Tallahassee, FL 32399-1600 U.S.A.*

ORIN L. BASS

*South Florida Natural Resources Center, Everglades National Park, 40001 State Road 9336,
 Homestead, FL 33034-6733 U.S.A.*

GREGORY D. BOSSART

Harbor Branch Oceanographic Institute, 5600 U.S. 1 North, Ft. Pierce, Florida, 34946 and Falcon Bachelor Bird of Prey Center, Miami Museum of Science, 3280 South Miami Avenue, Miami, FL 33129 U.S.A.

KEY WORDS: *Bald Eagles; Haliaeetus leucocephalus; hematology; serum chemistry; Everglades; health assessment; Florida Bay, Florida.*

Serum chemistry analysis involves the measurements of naturally-occurring enzymes and compounds, which are the result of metabolic and other physiological processes in the blood of birds (Harrison and Harrison 1986). The levels of several chemical compounds in the blood can be used in the diagnosis of the health status of individuals (Harrison and Harrison 1986).

More emphasis is being placed on the blood as a health-monitoring tool for wild birds (e.g., Dawson and Bortolotti 1997, Newman et al. 1997, Olsen et al. 2001, Balbontin and Ferrer 2002). Reference values are being established for plasma protein using electrophoresis as a diagnostic and prognostic means of assessing the health of several raptor species (Tatum et al. 2000). Establishing normal baseline values for the serum chemistries of free-ranging birds of prey will be important for future comparisons of population health. Interpreting serum chemistries must be done with scrutiny because age, sex, nutritional status and environmental conditions, circadian rhythms, and plasma and serum storage methods may influence these values (Ferrer 1993, Bustamante and Traviani 1993, Boal et al. 1998). Until more is known about

serum chemistries and their applications as a monitoring tool for free-ranging raptors, these results should complement and be used with good ecological data for population assessments (Newman 1997).

Hematological analysis provides valuable information concerning the health status of an individual animal. For example, packed cell volume (PCV) is a good indicator of red blood cell mass (Howard and Matsumoto 1977), but age, sex (Boal et al. 1998), molt, reproductive activity, migration, dehydration, and diseases can affect avian PCVs (Carpenter 1975, Heidenreich 1997, Morishita et al. 1998). To date, there have been few clinical studies of serum chemistries of free-living birds. Normal chemistry values are extrapolated primarily from psittacines (parrots, macaws) and other domesticated fowl (poultry) living in captivity (Newman et al. 1997).

The objective of this cooperative study was to determine selected clinicopathologic parameters for nestlings of free-ranging Bald Eagle (*Haliaeetus leucocephalus*). Since knowledge of the basic physiology of these animals is limited, this protocol will contribute towards the establishment of 20 “normal” baseline hematological and serum values for Bald Eagle nestlings in Florida Bay, Everglades National Park, Florida, U.S.A.

METHODS

Study Site. The scope of this research involved monitoring multiple islands in Florida Bay, Everglades National Park (Fig. 1). The Florida Bay estuary (latitude 25°4'N and longitude 80°47'W) lies between the southern portion of the Florida peninsula to the north, the Florida Keys to the east and south and the Gulf of Mexico to the west. Nests were located using historical data from the South Florida Natural Resources Center of the Ever-

¹ Present address: Institute of Wildlife Sciences, 10910 Cameron Ct., Suite 103, Davie, FL 33324 U.S.A.; e-mail address: bkmealey@aol.com

² Present address: U.S. Fish and Wildlife Service, Division of Migratory Bird Management, 4401 N. Fairfax Drive, Arlington, VA 22203 U.S.A.



Figure 1. The study site where the nestling Bald Eagles were sampled for serum chemistry between 1992 and 2001 was located in Florida Bay, Everglades National Park, Florida.

glades National Park or visually by following adults to the nest. The heights of the nests were ca. 1–10 m from the ground and built primarily on the black mangrove tree (*Avicennia germinans*). Surveys were conducted using an inflatable boat and fixed-wing aircraft. The keys on the eastern side of the bay had primarily flooded interiors, but the western keys of the bay were relatively vegetated and dry. The narrow shorelines of the eastern keys are spotted with sandy berms, which are fairly lush with dune plants including sea lavender (*Tournefortia gnaphalodes*), bay cedar (*Suriana maritima*), buttonwood (*Conocarpus erecta*), white mangroves (*Laguncularia racemosa*), bitter panic grass (*Panicum amarum*) and coast sandbur (*Cenchrus incertus*). The western keys were primarily fringed with the red mangrove (*Rhizophora mangle*), with the exception of Sandy Key, which had a sandy shoreline.

Aging and Sexing. Nests containing Bald Eagle nestlings 35–45 d old were visited from 1 January–1 May, from 1992–2001. Nestling development was monitored chronologically or through feather formation during repeated nest visits (Bortolotti 1984). No attempts were made to identify gender of nestlings because blood sampling occurred at 35–45 d. Sex determination using bill depth and foot length measurements may be applied when chicks are 60 d old (Bortolotti 1984). Clinical blood sexing techniques were not applied in this study. The nests were rarely monitored more than three times. Each nest was visited only once for blood sampling.

Blood Samples. When possible, blood was collected primarily in the mornings. Tides and weather played an extremely significant role when attempting to reach the islands. Circadian rhythms were considered prior to sampling, but occasionally the window within a 10-d period

to reach an island was extremely narrow, and therefore, samples were taken opportunistically. Nestlings were hooded with a traditional falconry hood manufactured by Northwoods, Inc. (Rainier, WA) and removed from the nests by the investigators. Blood was extracted from the brachial vein (Cooper 1985, Hoysak and Weatherhead 1991). The area surrounding the vein was cleaned with 70% isopropyl alcohol and a sterile 22-, 23-, or 25-gauge needle attached to a 3-ml syringe was used to extract 1–3 ml of blood from each nestling. All blood extraction sites had pressure applied and were observed for approximately 5 min post procedure to ensure clotting prior to placing the nestling back into the nest (Hoysak and Weatherhead 1991). We returned to each nest ca. 7–10 d post sampling, when possible, to reevaluate the nestlings' condition.

Blood samples were placed in small 1-ml red top plastic microtainer tubes with a serum separator, (Becton Dickinson Co., Franklin Lakes, NJ) and heparinized hematocrit, made by Jorgensen Laboratories, Inc., (Loveland, CO), tubes and allowed to clot for 15 min prior to centrifugation. Samples were spun for ca. 20 min with a portable Mobilespin centrifuge (Vulcan Technologies, MO) with a relative centrifugal force of $1100 \times g$. Centrifuging was complete when the serum separator distinctly walled off the serum from the red blood cells. The serum was transferred with a pipette to another blood tube to prevent hemolysis. Field samples were placed in an ice cooler and later frozen. Samples were stored at -16.1°C and analyzed within 30 d.

Serum Samples. Eaglet sample sizes varied for each serum chemistry test depending on the amount of serum available. Thus, an adequate amount of serum was not available to measure all parameters, and sample sizes varied. One hematological, packed cell volume (PCV) and nineteen serum chemistries were determined including, total protein (TP), albumin (ALB), aspartate aminotransferase (AST), alanine aminotransferase (ALT), alkaline phosphatase (ALKP), lactate dehydrogenase (LDH), creatine kinase (CK), uric acid (URIC), calcium (Ca^{2+}), phosphorus (PHOS), glucose (GLU), total bilirubin (TBIL), blood urea nitrogen (BUN), creatinine (CRSC), sodium (Na^+), potassium (K^+), chloride (Cl^-), carbon dioxide (CO_2), and cholinesterase (CHE). Blood samples were analyzed on a Kodak Ektachem DT II System (Johnson and Johnson, Rochester, NY). Ektachem controls were run once a week to assure quality analysis control with all samples. Mean values and standard deviations were determined using JMP SAS (1994) statistical discovery software.

RESULTS AND DISCUSSION

We collected samples from 151 Bald Eagle chicks from 22 nests between 1992 and 2001. Our blood sampling studies did not have visible adverse affects on the health or fledging of the eaglets. The sampling area was devoid of markings and infections confirming the lack of any adverse effects from our blood sampling technique. Eaglet inactivity generally lasted for 20 min after sampling. After that time eaglets sat up and started to call for food. The values for several serum parameters were variable, especially for LDH, CK, ALKP, AST, and URIC (Table 1).

Table 1. Hematological and serum chemistry values for Bald Eagle nestlings in Florida Bay, Everglades National Park.

MEASURE	N	MEAN ± SD	RANGE
PCV (%)	105	32.74 ± 4.16	17.0–42.0
GLU (mg/dl)	128	223.03 ± 27.37	150.0–292.0
PHOS (mg/dl)	151	6.31 ± 1.3	3.2–11.4
TP (g/dl)	125	3.28 ± 0.98	1.4–10.4
URIC (mg/dl)	147	13.46 ± 5.88	4.3–31.2
ALB (g/dl)	116	1.48 ± 0.43	1.0–3.2
ALKP (U/L)	123	147.57 ± 51.96	35.2–322.0
AST (U/L)	129	132.73 ± 48.04	46.0–357.0
ALT (U/L)	104	17.11 ± 7.41	3.0–42.0
Ca ²⁺⁺ (mg/dl)	148	9.39 ± 2.24	3.6–21.4
CHE (U/ml)	117	1.29 ± 0.31	0.3–2.5
CK (U/L)	117	1268.71 ± 557.69	473.2–3190.0
LDH (U/L)	79	2547.63 ± 965.22	1045.0–7479.0
CRSC (mg/dl)	42	0.24 ± 0.11	0.1–0.5
TBIL (mg/dl)	59	1.24 ± 1.06	0.3–4.1
BUN (mg/dl)	75	13.41 ± 10.79	2.0–44.0
Na ⁺ (nmol/L)	135	135.85 ± 11.13	99.0–164.0
Cl ⁻ (mmol/L)	136	104.98 ± 10.11	67.0–127.0
K ⁺ (mmol/L)	132	4.28 ± 1.82	2.2–9.7
CO ₂ (mmol/L)	117	18.9 ± 4.79	6.0–34.0

Currently the interpretation of avian biochemistries is difficult due to the lack of controlled studies and available references. Raptor biologists and wildlife veterinarians must also be aware that values between adults, juveniles, and nestlings may vary significantly (Boal et al. 1998). Collected data provide baseline parameters of free-ranging Bald Eagle nestlings in Florida Bay (Table 1). Even though raptor nestling serum values are not well-documented in the literature, the results of this study appear to be within the reported parameters for other free-ranging raptor nestlings.

The normal PCV ranges for parrots (Psittacidae) and other domestic birds is 37–53% (Harrison and Harrison 1986), seabirds 39–45% (Newman 1997, Work 1999), and for captive adult Bald Eagles 35–50% (Ivins et al. 1978). In other studies of free-ranging raptors, PCV are very variable (Balasch et al. 1976, Hunter and Powers 1980). This variation may be due to age and sex, migrating status, and reproduction (Boal et al. 1998, Stein et al. 1998). Our results showed that PCV mean values for the eaglets of 32.74% (Table 1) in this study fall within the range (31–38%) of free-ranging nestling eagles in Chippewa National Forest (CNF) (Redig et al. 1983) and nestlings in the lower peninsula of Michigan (Bowerman et al. 2000). In contrast, results for PCV mean values for free-ranging nestling Cooper's Hawks (*Accipiter cooperii*) was 42.2% for females and 38.7% for males (Boal et al. 1998).

Most normal avian values for total protein range between 3.0 and 5.0 g/dl. Values that fall below 2.5 g/dl may reflect parasitism, stress, or starvation. Values greater

than 5 g/dl may indicate dehydration, shock, or infection (Harrison and Harrison 1986). TP values in this study ranged 1.4–10.4 g/dl with a higher variation than those in Michigan (Bowerman et al. 2000). The mean values for TP in Florida Bay 3.28 g/dl were similar with the study sites in Michigan at 3.4 g/dl, but lower than results from CNF at 4.7 g/dl (Redig et al. 1983).

Uric mean and range values for Bald Eagle nestlings in Florida Bay were higher than the Bonelli's Eagle (*Hieraetus fasciatus*) nestling mean values of 7.77 mg/dl (684.2 umol L⁻¹) for males and 9.4 mg/dl (827 umol L⁻¹) for females (Balbontin and Ferrer 2002). High levels of uric acid in free-ranging eagle nestlings may be attributed to food stress (Ferrer 1994). GLU mean levels in eaglets in Florida Bay are lower than those in Michigan (280 mg/dl), but both fall within the normal range of 200–500 mg/dl for captive birds. Electrolytes results for Na⁺, K⁺, and Cl⁻ in Florida Bay were within the ranges of other Bald Eagle nestling studies (Redig et al. 1983, Bowerman et al. 2000). There were variations when compared with the Bonelli's Eagle (Balbontin and Ferrer 2002) and below the values of several European raptors (Polo et al. 1992, Jenkins 1994, Stein 1998).

High variation of CK and LDH levels in this study may be due to the handling and physiology of nestling eagles and is in accord with the results found in free-living Bonelli's Eagle, Booted Eagles (*Hieraetus pennatus*), and the Spanish Imperial Eagles (*Aquila adalberti*) (Polo et al. 1992, Balbontin and Ferrer 2002, Casado et al. 2002).

CHE levels <0.9 u/ml are considered depressed and

likely due to intoxications (Porter 1993, Heatley and Jowett 2000). In 1997, one eaglet from Frank Key and one from Park Key were found to have depressed levels of CHE. Both eaglets fledged successfully. It is possible that these eaglets may have been exposed to organophosphates after consuming avian prey brought in by the parents. In contrast, Osprey (*Pandion haliaetus*) had CHE levels above 1.0 u/ml (B. Mealey unpubl. data). There is some question about the value of using CHE as an indicator for exposure to an organophosphate pesticide due to the variations in CHE levels over a short period of time (P. Mineau pers. comm.).

Reference values for PHOS in domestic birds are 2–6 mg/dl. The mean values of eaglets in Florida Bay (Table 1) were in the range of other Bald Eagle nestling studies (Redig et al. 1983, Bowerman et al. 2000) and similar to the mean results for adult Spanish Imperial Eagles (5.8 mg/dl), Golden Eagles (*Aquila chrysaetos*; 4.7 mg/dl), Griffon Vultures (*Gyps fulvus*; 4.3 mg/dl), and Egyptian Vultures (*Neophron percnopterus*; 7.3 mg/dl) (Polo et al. 1992, Dobado-Berrios et al. 1998).

ALKP mean results for free-ranging eagle nestlings in Florida Bay (147.5 U/L) were similar to adult eagles and lower than found by Bowerman (2000) in Michigan (449 U/L) and Balbontin (2002) in Spain (2148 UI L⁻¹).

Evaluation of serum chemistries offers wildlife biologists and federal and state agencies an additional way of monitoring the health of free-ranging raptor populations. If there is an opportunity to gather additional data on blood serum parameters from a listed raptor population, then every effort should be made to enhance the existing pool of knowledge concerning such species. As with every technique, precautions should be taken to avoid any potential injury or undue stress to the animals.

Data interpretation from the serum chemistries is subject to debate because of the many variables that affect particular enzymes. Standardized protocols should be established and long-term studies on the baseline values of a particular species should be conducted. Areas in need of attention and further research with free-living raptors are: (1) the effects of capture and handling and how this stress may affect results; (2) how does age, sex, and season alter the serum values; and (3) the effects of nutrition on these serum value indicators. Evaluations of serum chemistries are in its infancy stage for free-ranging birds of prey. As further research is conducted, the information gathered will aid in the applications of serum chemistry analysis as a tool for the management of raptor populations.

RESUMEN.—El análisis de la química del suero esta comenzando a ser una herramienta de diagnóstico vital para evaluar la salud de las aves de presa en libertad. La química del suero de 151 polluelos de águilas calvas (*Haliaeetus leucocephalus*) en vida silvestre, fue medida de 1992–2001 en la bahía de la Florida, Parque Nacional Everglades. Medimos 19 valores de suero y un valor hematológico

(PCV) para establecer los parámetros normales de línea base para los aguiluchos. Los resultados de los valores de suero fueron consistentes con los resultados de otras poblaciones de aves rapaces en libertad.

[Traducción de César Márquez]

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LETTER

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LIVE MAMMAL PREY (*ZAEDYUS PICHYI*) IN A NEST OF THE BLACK-CHESTED BUZZARD-EAGLE (*GERANOAEETUS MELANOLEUCUS*)

Raptors bringing various kinds of live prey to their nests has been described by Spofford and Amadon (1993, *J Raptor Res.* 27:180–184). These authors concluded that this behavior was accidental or incidental and nonadaptive. While live insects, lizards, and birds were reported as having been brought to the nests of several species, live mammal prey were not described by Spofford and Amadon (1993).

We report here an instance of a live piche (*Zaedyus pichiy*), a small species of South American armadillo, brought to a nest of a Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*) in southern Patagonia. The observation was recorded in Estancia “El Cuadro,” department Deseado, Santa Cruz province, Argentina (47°30'S, 68°W) during a study of the breeding biology of several raptors in southern Patagonia, Argentina, including Black-chested Buzzard-Eagle, between September 1987 and January 1988 (De Lucca and Saggese 1993, *Hornero* 13:302–305; De Lucca and Saggese 1995, *Hornero* 14:38–39; Saggese and De Lucca 1995, *Hornero* 14:21–26; and Saggese and De Lucca 2001, *Hornero* 16:77–84). The study area is within the Central Patagonic District—Patagonian province phytogeographic region (Cabrera 1976, *Regiones Fitogeográficas argentinas*, ACME Ediciones, Buenos Aires). A detailed description of the study area and nest site characteristics can be found in Saggese and De Lucca (2001).

On 17 November 1987, we observed the nest for 1 hr 45 min between 1915 H and 2100 H (sunset) from a blind placed 50 m in front of the cliff, with the aid of 7–10 × 50 binoculars. The nest was located at 12.5 m above the base of a basaltic cliff 25 m high. At the beginning of the observation period, the female was brooding a 5-d-old nestling on the nest. At 1944 H, the female suddenly stood up on the nest. At this time, we observed one adult-sized piche on the nest, walking slowly from one side of the nest to the other. The female buzzard-eagle remained standing up on the nest structure and made no attempt to grab the piche, but simply watched it walk across the nest. After 9 min, without any obvious change in the buzzard-eagle’s behavior or attitude, the piche stopped walking and remained still on the front side of the nest, facing the cliff. Some seconds later, the piche fell out of the nest to the bottom of the cliff. At this point, the female buzzard-eagle showed interest, stood on the edge of the nest and looked down. Approximately 5 min later, she fed the young with food that was already in the nest for 16 min and then started to brood the nestling again until the end of the observation period. The male was perched on the cliff or away from the nesting area during this observation and was not involved in this event. During the 385 hr of close monitoring of this nest, no other incidents like this were observed.

We were not sure whether the piche jumped out of the nest or accidentally fell, but our impression was that the piche jumped out. To avoid disrupting the eagles, no attempt was made to approach the nest site to find the piche. The final outcome of the fallen piche was unknown, but the height from which the piche fell down and the large field of rocks at the base of the cliff, make the possibility of survival doubtful. At the end of the study, three piche’s carapaces and bones were found among other prey remains at the base of this nesting cliff. Upon gross examination, no damage was found on the shells of the remains. Piche remains were found in other nests with nestlings, consumed as prey, as well as at the bottom of other nesting cliffs, but if they were consumed by the eagles or by other scavengers after falling from the nest could not be determined.

Piches were recorded as prey in several nests studied in this area, being 5.6% of prey remains found in three buzzard-eagle nests and 4.8% of prey at another nest (Saggese and De Lucca 2001). Massoia and Pardinhas (1986, *Acintania* 23:24–26) and Hiraldo et al. (1995, *Wilson Bull.* 107:675–685) also reported piches as prey of these buzzard-eagles.

Piches are small mammals with a total body length of 260–335 mm, a tail length of 100–140 mm, and a mass of ca. 1–2 kg (Nowak 1999, Walker’s Mammals of the World. Johns Hopkins Univ. Press, Baltimore, MD, and London, U.K.). Like other armadillos (Dasypodidae), they have a bony shell on the dorsal part of their bodies, covered with a carapace (keratin layer) which gives them some protection from predators (Nowak 1999). The piche’s protective shell is absent ventrally, where soft, naked skin is present. This is the only accessible area to most predators. Additionally, the piche shows a defensive behavior consisting of pulling its extremities inside its shell and pressing its body against the ground (Nowak 1999), which makes it difficult for predators to reach the soft ventral parts of its body.

Because piches are known as prey of these raptors, and owing to the inaccessibility of this cliff and nest, we suggest

that this live piche was brought to the nest by one of the buzzard-eagles, probably the male. As far as we know, this is the first recorded instance in which a live mammal prey item was brought to a raptor nest and escaped, although the ultimate fate of this prey was not known. The presence of this live armadillo in the nest may reflect the difficulty of a raptor killing it, due to the piche's armor and protective behavior.

That prey animals escape from predators by different mechanisms is widely recognized (e.g., Curio 1976, *The ethology of predation*, Springer, Berlin, Germany; Endler 1986, *Defense against predators*, pages 109–134 in M.E. Feder and G.V. Lauder [Eds.], *Predatory-prey relationship*, Univ. of Chicago Press, Chicago, IL U.S.A.). Spofford and Amadon (1993) also mentioned several instances in which living prey sometimes escaped from their predators after capture. Gehlbach (1994, *The Eastern Screech Owl*, Texas A&M Univ. Press, College Station, TX U.S.A.) reported that blind snakes (*Leptotyphlops* sp.) hunted by Eastern Screech Owls (*Otus asio*) frequently survive the attack thanks to their writhing defensive behavior, smooth cylindrical body and repellent secretions, after which some live commensally in the owl's nest, feeding on fly larvae and pupae.

Of course, no information exists concerning the frequency of escapes by piche from buzzard-eagles at their nests. The advantages of surviving an eagle attack because of the piche's carapache cover and then escaping from the nest are obvious, and these behavior and defense mechanisms may explain the low number of this species in the diet of Black-chested Buzzard-Eagle, despite the fact that piche seem to be fairly common in the Patagonia throughout the range of these raptors. Alternatively, the eagles may avoid hunting these armadillos because they are difficult to catch and kill. Further observations are needed in order to verify at what frequency are live armadillos brought to nest by Black-chested Buzzard-Eagle and under which circumstances.

We want to thank Fundación Vida Silvestre Argentina, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Asociación Ornitológica del Plata, Administración de Parques Nacionales, Intendencia and Museo del Hombre de Caleta Olivia for providing financial and technical assistance during the study. Sue Kirchoff made helpful comments on an early version of the manuscript and Dr. D. Mech generously provided literature about anti-predatory behavior and escape mechanisms. Finally, we thank D. Whitacre for his careful review and comments on this manuscript and for providing literature.—**Miguel D. Saggese, The Raptor Center, University of Minnesota, 1920 Fitch Avenue, Saint Paul, MN 55108 U.S.A., e-mail address: sagge001@umn.edu; and Eduardo R. De Lucca, Rosales 3180, La Lucila, (1636), Buenos Aires, Argentina.**

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BOOK REVIEW

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Raptors of Eastern North America. By Brian K. Wheeler. 2003. Princeton University Press, Princeton, NJ. 456 pp., 559 color photographs, 37 maps. ISBN 0-691-11598-2. Cloth, \$45.00. **Raptors of Western North America.** By Brian K. Wheeler. 2003. Princeton University Press, Princeton, NJ. 560 pp., 622 color photographs, 56 maps. ISBN 0-691-11599-0. Cloth, \$49.50.—These companion guides are intended for the moderate-to-expert-level raptor enthusiast. The exquisite photos in the books clearly illustrate all of the confusing age, sex, and geographic variants for the 34 diurnal raptor species in North America. These books also contain an incredible amount of new natural history and conservation-related information.

The eastern guide provides detailed species accounts for 26 species (including the two vultures) that occur regularly east of the Mississippi River; the western guide treats a total of 33 species. Each account includes information on molt, plumage traits (by age, sex, color morph, and subspecies), habitat preferences, status and distribution, migration patterns and timing, feeding behavior, courtship and nesting, flight behavior, and conservation efforts. The range maps are accurate and exceptionally detailed and include subspecies where appropriate. Literature citations are listed at the end of each account.

I was immediately struck by the comprehensive research effort undertaken for the status and distribution accounts. When available, up-to-date continental population estimates are given, as well as statewide and regional numbers. For example, the western guide reveals that 600 pairs of the Peale's Peregrine Falcon (*Falco peregrinus pealei*) remain in Alaska, and the total world population of this subspecies is only 700 pairs. Wheeler frequently cites recent totals from the autumn migration counts in Veracruz, Mexico, to substantiate his continent-wide population estimates.

I especially enjoyed reading the section in each species account on conservation. I learned that Mexico plans a total ban on DDT use by 2006. I

read about efforts to restore Golden Eagles (*Aquila chrysaetos*) to the southeastern U.S.; indeed, Georgia hacked 117 eagles (mostly from Wyoming) from 1984 to 1992. I also found a complete list of the mortality factors that are affecting reintroduced populations of California Condors (*Gymnogyps californianus*).

Wheeler augments his discussion of migration for each species with the latest satellite telemetry data and results from various unpublished reports. For example, he mentions a Peregrine Falcon tracked by the Canadian Wildlife Service that migrated from Edmonton, Alberta, to Mazatlan, Mexico (a distance of 3500 km), in less than 12 days!

The stunning photographs are the backbone of these two guides. Every plumage variation for each species is abundantly illustrated. The treatment of the Red-tailed Hawk (*Buteo jamaicensis*) is particularly exhaustive, with a total of 82 photos (including 28 for the Harlan's subspecies) and five range maps.

I detected no glaring inaccuracies in either book. I do have a couple of minor criticisms, however. First, some of the identification characteristics mentioned might work well for perched birds seen through a spotting scope (e.g., iris and bill color, facial markings), but identification of distant birds and birds in flight generally is not emphasized. Second, the photos and corresponding captions do not always point the reader immediately to those characters that might best be used to distinguish a particular age, sex, subspecies, or species. Finally, some key features for distinguishing similar species are mentioned only briefly or omitted altogether (this was especially true for members of the genus *Accipiter*).

For these reasons, I do not recommend these books as stand-alone field guides for North American raptors. They are outstanding adjuncts to your Clark and Wheeler (Peterson's *Hawks Guide*), Dunne et al. (*Hawks in Flight*), or Wheeler's own *Photographic Guide*, and they go far beyond these field guides by providing detailed status and distributional data, as well as fresh natural history and conservation information.

Although these two books may seem a bit pricey, when one appreciates the exceptional quality of

the photos and the tremendous volume of useful information contained in each species account, I believe the price is very reasonable (if not a bargain). Anyone interested in the identification, natural history, and conservation of North American

diurnal raptors will not want to be without these companion volumes in his/her library.—**Stephen W. Hoffman, Audubon Pennsylvania, 100 Wildwood Way, Harrisburg, PA 17110 U.S.A.**

MANUSCRIPT REFEREES

The following people reviewed manuscripts for the *Journal of Raptor Research* in 2003. Peer review plays a vital role in the publishing process and in improving the quality of the Journal. The editorial staff would like to thank the following people for reviewing manuscripts this past year. The names of those who reviewed two or more manuscripts are indicated with an asterisk.

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